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ESTIMATION OF THE GASEOUS CO_2 CONCENTRATION IN INTERCELLULAR SPACES DURING PHOTOSYNTHESIS

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The equation which Browne and Escombe (1900) derived to estimate diffusive capacity of plant stomata contains an assumption of CO_2 gradients across the stomata which is quite unreasonable. A slightly modified form of the equation is reproduced below to demonstrate this unreasonable assumption:

$$Q = \frac{D\,A\,(C_o - C_s)}{L + F} \qquad (1)$$

In which,

Q is the CO_2 transport per cm.^{2} of leaf per second
D is the diffiusivity of CO_2 in air
A is the stomatal area in cm^2 per cm.^{2} of leaf
C_o is the CO_2 concentration in air outside the leaf
C_s is the CO_2 concentration in air inside the leaf
L is the length of the stoma tube
F is a correction introduced because the effective tube length is greater than the actual tube length. In tubes having a circular cross-section this correction is a function of tube radius, $F = \frac{\pi\, r.}{2}$

The unreasonable assumption made by Browne and Escombe was the assumption that C_s equalled zero. The unreasonable nature of this assumption has been recognized (Spoehr, 1926, p. 77) but although a few investigators have tried to apply the equation to specific plant leaves (Maskell, 1928; Stalfelt, 1935) they retained this assumption and I have found no reported attempts to obtain more reasonable estimates of the value of CO_2 concentration within the intercellular spaces of leaves during photosynthesis.

An inspection of equation (1) shows that it can be used to estimate the concentration drop ($C_o - C_s$) across the stomata if the value of Q is specified, thus:

$$C_o - C_c = \frac{Q\,(L + F)}{D\,A} \qquad (2)$$

If we use the following values, all reasonable approximations for an average leaf under conditions favorable for photosynthesis:

$Q = 0.06 \times 10^{-6}$ g./cm.^{2}/sec. (20 mg./dm.^{2}/hr.)
$L = 15 \times 10^{-4}$ cm.
$F = 8.8 \times 10^{-4}$ cm.
D = 0.15 cm.^{2}/sec. (assuming a temperature of 20° C and a barometric pressure of 76 cm. Hg)
A = 0.01 cm.^{2}/cm.^{2} of leaf.

Then $(C_o - C_s)$ amounts to 0.095×10^{-6} g./cm.^{3}. This represents a concentration drop of about 16 percent, assuming a CO_2 concentration of 0.59 μg./cm^3. (0.03 vol. percent) in the air outside the leaf.

There are two questions concerning this application of the equation which must be raised: (1) what is the nature of the correction F, and (2) how does the influence of neighboring stomata affect the validity of the equation. To examine these questions I have made an analysis of gradients across a stoma tube based on the diagram of figure 1. The stomatal dimensions in this diagram are the same as in the above application of equation (2). The stoma tube has a length of 15 μ and a radius of 5.6 μ, giving it a cross-sectional area of 100 μ^2. On either side of the stoma hemispheres of influence are portrayed. The external hemisphere has an area of 10,000 μ^2, a limit set by the fact that stomata occupy 1 percent of the leaf area. The internal hemisphere has an area of 100,000 μ^2, a limit set by the fact that the surfaces of cells bordering on intercellular spaces present about 10 times as much area as the leaf exterior (Miller, 1938, p. 414). The regions of influence are assumed hemispherical to simplify mathematical treatment. The hemispherical shape of diffusion shells also suggests such a diagram.

Figure 1 can be used to analyze CO_2 concentration gradients across the stoma tube and its hemispheres of influence. Across the stoma tube the gradient is constant and can be expressed as:

$$\frac{dc}{dx} = \frac{C_a - C_b}{L} \tag{3}$$

where C_a is the CO_2 concentration at the outer end of the stoma tube, C_b is the concentration at the inner end of the tube, and L is the length of the tube. Between the ends of the stoma tube and the surfaces of the hemispheres of influence the gradients are variable, being inversely proportional to the square of the distance from the small hemispheres portrayed at the ends of the stoma tubes (cf. Verduin, 1949). The area of these small hemispheres is equal to the area of the stoma. The concentration gradient at any point within the external hemisphere is given by the equation:

$$\frac{dc}{dx} = \frac{k}{x^2} \tag{4}$$

where k is a proportionality constant. The concentration drop across the external hemisphere of influence can be estimated using the definite integral:

$$C_o - C_a = \int_{x=4\times10^{-4}}^{x=40\times10^{-4}} \frac{k}{x^2}\,dx = \left[-\frac{k}{x}\right]_{4\times10^{-4}}^{40\times10^{-4}} \tag{5}$$

The concentration gradient at any point in the internal hemisphere of influence is given by the equation:

$$\frac{dc}{dx} = -\frac{k}{x^2} \tag{6}$$

the minus sign indicating that the concentration decreases as x increases. The concentration drop across this hemisphere is given by:

$$C_b - C_s = -\int_{x=126\times10^{-4}}^{x=4\times10^{-4}} \frac{k}{x^2}\,dx = -\left[-\frac{k}{x}\right]_{126\times10^{-4}}^{4\times10^{-4}} \tag{7}$$

(The assault made by Romell (1927), on this portion of the gas diffusion path yielded results which do not differ significantly from that of the simple analysis presented here. Attempts to specify the magnitude of the invasion coefficient across the cell wall boundary, and of the diffusivity and length of diffusion path

in the cytoplasm, were premature then and remain so today.) We can evaluate k, for the rate of transport specified above, noting that the concentration gradient at the surface of the outer hemisphere of influence is valid for the entire leaf, hence, $\frac{dc}{dx} = \frac{Q}{D} = \frac{0.06\times10^{-6}}{0.15} = 0.4\times10^{-6}$g/cm^4., when $x = 40\times10^{-4}$cm. Substituting in (4) we obtain $k = 6.4\times10^{-12}$. The concentration drop across each hemisphere of influence can now be computed.

$$C_o - C_a = \left[\frac{6.4\times10^{-12}}{4\times10^{-4}} - \frac{6.4\times10^{-12}}{40\times10^{-4}}\right] = 1.44\times10^{-8}\text{g./cm.}^3$$

$$C_b - C_s = \left[\frac{6.4\times10^{-12}}{4\times10^{-4}} - \frac{6.4\times10^{-12}}{126\times10^{-4}}\right] = 1.55\times10^{-8}\text{g./cm.}^3$$

The concentration drop across the stoma tube can be computed noting that the gradient here is 100 times that computed for the entire leaf, or 0.4×10^{-4} g./cm.^{4} Substituting in (3) we obtain,

$C_a - C_b = 15\times10^{-4}\times0.4\times10^{-4} = 6\times10^{-8}$ g./cm.^{3}

The total concentration drop $C_o - C_s$ then is the sum of these three components, $(1.44+6.00+1.55)\times10^{-8} = 9.0\times10^{-8}$, or 0.090×10^{-6}g./cm.^{3}

This estimate agrees closely with the value of 0.095×10^{-6} obtained from equation (2).

The above analysis clarifies the nature of the correction F in equations (1) and (2). The correction accounts for the gradients within the hemispheres of influence. In equation (2) therefore C_o represents the CO_2 concentration at the surface of the outer hemisphere of influence, and C_s represents the concentration at the surface of the cells bordering on the intercellular spaces. They do not represent concentrations at the immediate ends of the stoma tube.

So far nothing has been said about the effect of neighboring stomata on the validity of equation (2). In the analysis based on figure 1 the problem of the mutual influence of stomata is solved by designating the limits of the hemispheres of influence. Molecules from neighboring hemispheres will, of course, enter the hemisphere in question, but their effect will be cancelled by losses to neighboring hemispheres. The major influence of neighboring stomata is taken into account in equation (2) in essentially the same way as in the analysis based on figure 1. For example: in equation (2) if the area represented by the stomata (A) is doubled by doubling the number of stomata, the value of $C_o - C_s$ is reduced to 0.047×10^{-6} g./cm.^{3}. In the analysis based on figure 1 such a doubling of the stoma population would reduce the area of the hemispheres of influence by a factor of 2, the gradient at the stoma would be one-half as high as before, the upper limit in equation (5) would become 28.2×10^{-4}, the lower limit in (7) would become 89.2×10^{-4}, k would be 3.2×10^{-12} yielding a $C_o - C_s$ value of 0.0445×10^{-6} g./cm.^{3}. So it appears that the effect of neighboring stomata is adequately accounted for in equation (2) by the factor A, and that equation (2) provides a reliable estimate of the CO_2 concentration drop across the stoma tubes plus their hemispheres of influence. This statement is true for plant leaves because the stomatal areas represent so small a fraction of the leaf area. If stomata were so numerous that they represented a large fraction of the leaf area, then equation (2) and the analysis based on figure 1 yield more widely divergent estimates. For example: if $A = 0.5$ then $C_o - C_s$ from equation (2) becomes 0.0019×10^{-6} g./cm.^{3}, but in the analysis based on figure 1 it would amount to 0.0015×10^{-6}. These estimates differ by about 20 percent compared to only a 5 percent discrepancy when using stomatal areas similar to those observed in nature.

If one assumes that the CO_2 concentration at the surfaces of the external hemispheres of influence is equal to that in the outside air, then equation (2) can provide an estimate of the CO_2 concentration at the surfaces of the cells bordering on the intercellular spaces. Such an assumption requires high air turbulence near the leaf, but under outdoor conditions turbulence is high (Jeffreys, 1918) and the CO_2 concentration of the outside air is probably maintained to within one millimeter of the leaf. So under completely natural conditions a leaf exhibiting photosynthesis rates of 20 mg./dm.^{2}/hr. probably would have an internal CO_2 concentration of about 0.1 μg./cm.^{3} less than the CO_2 concentration of the outside air.

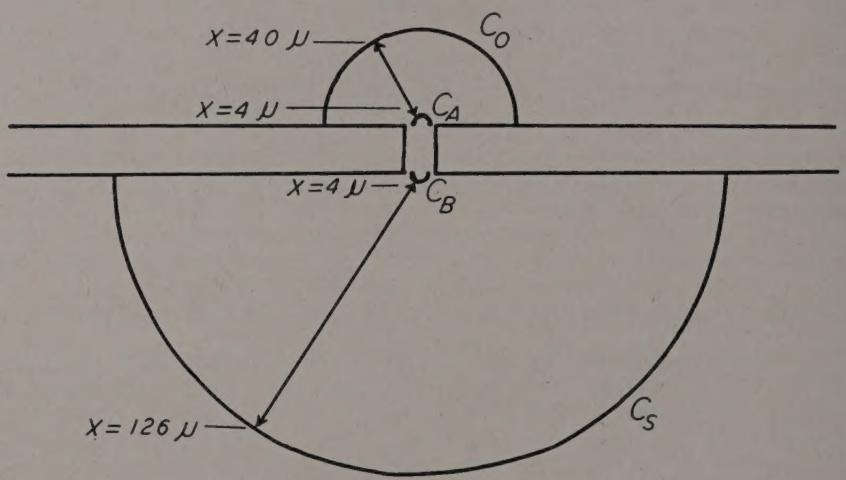

FIGURE 1. Diagram used to analyze concentration gradients across stoma. The outer hemisphere of influence represents an area of 10,000 μ^2 (radius, 40 μ) the inner hemisphere of influence represents an area of 100,000 μ^2 (radius, 126 μ) the stoma tube has a cross section of 100 μ^2 and is 15 μ in length. C_o represents the CO_2 concentration at the surface of the outer hemisphere of influence, C_a that at the outer end of the stoma tube, C_b at the inner end of the stoma tube, and C_s at the surfaces of the cells bordering on the intercellular spaces.

It was stated above that Browne and Escombe's assumption that $C_s = O$ was unreasonable. Measurements of the CO_2 compensation point (Rabinowitch II, 1, p. 898) suggest that C_s cannot be reduced much below 0.2 μg./cm.^{3}, so an estimate of the maximal photosynthesis rates possible under outdoor conditions with the stomatal characteristics specified above can be made by setting $C_s = 0.2 \times 10^{-6}$ and $C_o = 0.59 \times 10^{-6}$ in equation (1), thus:

$$Q = \frac{0.15 \times 0.01 \times (0.59 - 0.20) \times 10^{-6}}{23.8 \times 10^{-4}} = 0.25 \times 10^{-6} \text{ g./cm.}^2\text{/sec. or 90 mg./dm.}^2\text{/hr.}$$

It is probably a coincidence that this value is close to the highest maximal rates reported under near-natural conditions (Rabinowitch II, 1, p. 1001).

Most of our knowledge of photosynthesis under near-natural conditions is based on experiments in which the leaves were surrounded by transparent chambers through which air was drawn. The air flow through such chambers is not high enough to create turbulence similar to that in outdoor air. Heinicke and Hoffman (1933) for example, adopted a flow rate of about 2.5 l./cm.^{2} leaf/hr. (about 7 m./min. with their leaf cups) because this flow rate yielded CO_2 absorption by hydroxide solutions equalling the absorption rate by such solutions when exposed in a quiet room. Most investigators have used lower rates of air flow. In a

quiet room the air near an absorbing surface suffers significant CO_2 depletion. A fair quantitative estimate of this effect can be made by comparing the absorption rate for a hydroxide solution in quiet air with the rate in moving air, as Browne and Escombe did. They found that the maximum rate in moving air was 0.177 cm.^{3}/cm.^{2}/hr., while the quiet air rate was 0.120. If one assumes that the maximum rate represents a CO_2 concentration at the absorbing surface equal to 0.59 μg./cm.^{3}, then the CO_2 concentration at the absorbing surface under quiet conditions must have been about 0.40 μg./cm.^{3} A similar CO_2 concentration at the absorbing surface can be assumed for the experiments of Heinicke and Hoffman, and it is possible then to compute the effective length of the diffusion path over which a diffusivity of 0.15 cm.^{2}/sec. can be considered valid under their experimental conditions. Specifically, in their experiment with 0.2 N KOH a rate of 24.4 mg./dm.^{2}/hr. (0.068×10^{-6} g./cm.^{2}/sec.) was associated with a mean CO_2 concentration of 0.53 μg./cm.^{3} in the air stream passing over the solution. The effective length of the diffusion path can be estimated as:

$$\frac{0.15\times(0.53-0.40)\times10^{-6}}{0.68\times10^{-6}} = 0.29 \text{ cm.}$$

The drop in CO_2 concentration between the air in a leaf chamber (C_c) and the air at the surfaces of the external hemispheres of influence (C_o) can be approximated using the equation:

$$C_c - C_o = \frac{Q}{D}\times0.29 \tag{8}$$

Using the values of Q and D specified under equation (2) in equation (8) this drop in concentration amounts to

$$\frac{0.06\times10^{-6}}{0.15}\times0.29 = 0.12\times10^{-6} \text{ g./cm.}^3$$

In the photosynthesis studies of Heinicke and Hoffman photosynthesis rates of 20 mg./dm.^{2}/hr. were usually associated with mean CO_2 concentrations in the leaf chamber of about 0.50 μg./cm.^{3} The average CO_2 concentration at the surfaces of the cells bordering on the intercellular spaces (C_s) under such conditions would be estimated at $(0.50-0.12-0.09)=0.29$ μg/cm.^{3} This is approximately one-half the value for normal air, and the CO_2 concentration drop which occurs between the outer hemispheres of influence and the air in the chamber, is larger than the drop which occurs across the stomata.

The data of Stålfelt (1935) provide an opportunity to make similar computations for a wide range of stomatal areas, and the photosynthesis rates associated with them. Such computations are presented in table 1. The rate of air flow through Stålfelt's leaf chambers was about 4 m./min., so I have used equation (8) to provide estimates (conservative) of the concentration change ($C_c - C_o$) between the air in the leaf chamber and the surfaces of the external hemispheres of influence. The values of ($C_o - C_s$) were computed using equation (2). The values of A were approximated from Stålfelt's table 5 to correspond to the stomatal apertures listed in table 4. The values of C_c were computed from the data in table 4 knowing that the flasks used had a volume of 5.5 l., and that the CO_2 content of air outside the leaf chambers was approximately 0.59 μg./cm.^{3} The values of F were computed using the equation:

$$F = \frac{\pi}{2}\sqrt{\frac{A}{\pi\times8700}} \tag{9}$$

In this equation the stomata are assumed circular in cross-section. The number 8700 is based on Stålfelt's reported stomatal density of 87/mm^2 of leaf. The fact that *Avena* stomata are narrow slits makes the F values computed by this method somewhat smaller than they should be. It can be shown that the F value

for a narrow slit would be higher than that for a circular pore of the same area, but for the purpose of these computations equation (9) is regarded as a sufficiently close approximation. Stålfelt reported that the stoma tube length was about 10 μ. The reliability of this estimate was not indicated. It has been used to obtain the values of (L + F) in table 1.

Table 1 shows that the estimated values of ($C_c - C_o$) diminish, while the values of ($C_o - C_s$) increase as stomatal areas decrease. The net effect of these two concentration changes is such that the estimates of C_s are practically constant (0.37 μg./cm.^{3}) throughout the range of stomatal areas and CO_2 absorption rates listed there. The CO_2 concentration at the surface of the cells bordering on the intercellular spaces would seem to be considerably lower than that in normal air, but it was not proportional to stomatal area. The reduction in CO_2 absorption rate associated with reduced stomatal areas, therefore, was not caused by a reduction in CO_2 concentration at the boundary between gas and cell wall in the leaf, but reductions in CO_2 absorption rate occurred while this CO_2 concentration remained practically constant.

TABLE 1

Computation of C_s based on data from tables 4 and 9 of Stålfelt

Q μg./cm.^{2}/sec.	Stomatal width μ	Stomatal area cm.^{2}/cm.^{2} of leaf	Mean C_c μg./cm.^{3}	F μ	L + F μ	$C_c - C_o$ μg./cm.^{3}	$C_o - C_s$ μg./cm.^{3}	C_s μg./cm.^{3}
0.052	7.3	0.016	0.52	12.0	22.0	0.101	0.048	0.371
0.044	6.4	0.013	0.53	10.8	20.8	0.084	0.047	0.399
0.050	5.5	0.011	0.52	10.0	20.0	0.096	0.061	0.363
0.052	4.5	0.009	0.52	9.0	19.0	0.101	0.073	0.346
0.039	2.8	0.006	0.53	7.4	17.4	0.075	0.075	0.380
0.036	2.0	0.004	0.52	6.0	16.0	0.070	0.096	0.354
0.031	1.4	0.003†	0.54	5.2	15.2	0.061	0.105	0.374
0.017	0.5	0.001*	0.56	3.0	13.0	0.032	0.147	0.381

†Extrapolated by Stålfelt. *I extrapolated further to obtain the final value.

The concept of diameter proportionality of diffusion through small pores has frequently been invoked to explain the high diffusive capacity of stomata. An inspection of equation (1) shows that diffusive transport (Q) is proportional to pore area (A) divided by effective tube length (L + F). With circular pores A is proportional to diameter squared and F is proportional to diameter. If L is small compared to F then the quantity $\frac{A}{L + F}$ becomes approximately proportional to diameter. But in stomata L is not small compared to F, and table 1 shows that as stomatal areas diminish the magnitude of F also diminishes. The concept of diameter proportionality, therefore, has little bearing on stomatal diffusion. The high diffusive capacities of stomata are attributable to the increase in concentration gradients within their spheres of influence. Once this is taken into account it becomes evident that diffusion through stomata is a function of area just as it is in any other diffusion problem.

In my 1949 analysis of interference among stomata the effect of reduced interference as stomatal areas diminish was described. The effect appears in the present analysis in the diminishing values of F in table 1 as stomatal areas become smaller. Thus stomatal closure causes an increased concentration drop across the stomata and their hemispheres of influence, for a given rate of transport (Q) but the increase is less than would be predicted on the basis of stomatal area alone because the quantity (L + F) decreases.

The low values of C_s computed above imply that maximal CO_2 absorption rates occuring under completely natural conditions may be considerably higher than most of the maxima for near-natural conditions reported in the literature. Heinicke and Hoffman (1933) in their table 4 showed that increasing the air flow rate from 2.5 to 7.5 l./cm².hr. was associated with a photosynthesis increase from 22.1 to 30.8 mg./dm.²/hr. Most of this increase is probably attributable to an improvement in air turbulence in the leaf chamber, causing a shortening of the effective diffusion path between the CO_2 concentration in the chamber and the outer hemispheres of influence. There is no reason to believe that the turbulence in the latter case exceeded that of ordinary outdoor conditions. The importance of air turbulence within leaf chambers has not received adequate attention in studies of photosynthesis employing natural air supplies. It may be that this factor is responsible for the higher maximal rates reported by Russian investigators, and pointed out by Rabinowitch in his table 28.VI, p. 998–1001.

SUMMARY

An analysis of diffusion through stomata is presented which shows that the CO_2 concentration in air at the surface of the cells bordering on the intercellular spaces (C_s) of a leaf can be computed if the rate of CO_2 absorption and the stomatal dimensions are specified. Such computations indicate that in a leaf having average stomatal characteristics and absorbing 20 mg. of CO_2/dm.²/hr. under completely natural conditions C_s would be about 0.1 μg./cm.³ less than in the outside air. The maximal CO_2 absorption rate possible for such a leaf, computed by setting $C_s = 0.2$ μg./cm.³ (the CO_2 compensation point) would be about 90 mg./dm.²/hr. In experimental determinations of photosynthesis rates the air in leaf chambers is much less turbulent than outdoor air, and an important drop in CO_2 concentration occurs between the air in a chamber and the air near the leaf. In such experiments a CO_2 absorption of 20 mg./dm.²/hr. corresponds to a C_s of about 0.3 μg./cm.³, or approximately one-half the CO_2 concentration in normal air.

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This well illustrated booklet recounts in non-technical language the development of the Lake Hope region's varied mineral resources, as well as serving as a guide to the geology and topography of that area. It is available from the Division of Parks, 1106 Ohio Departments Building or from the Division of Geological Survey, Orton Hall, Ohio State University, both in Columbus, Ohio. F. W. F.

BUSINESS SIZE AS A FACTOR IN BUSINESS LEADER MOBILITY

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This paper deals with the relationship between origins of business leaders and the size of the organization under their control. Two tasks are undertaken: (1) the description of the association between the number of employees in a business firm and the occupational origin of its principal executive, and (2) the analysis of the significance of this association for the recruitment of business executives in future decades. The latter task is one aspect of the general problem of analysis of trends in social stratification in this society.

PROCEDURE

The subjects of this study are 220 business leaders – owners or chief executives of firms employing 100 or more workers - located in four U. S. cities. These individuals were respondents in a sample of 510 executives drawn at random from directories of business in Springfield and Worcester, Massachusetts, and Columbus and Toledo, Ohio. Data on the economic and social histories of the respondents and their fathers were obtained in part by mailed questionnaires, and in part by interviews with a one-third sample of prospective respondents who failed to return the questionnaire in two of the cities. The final returns consisted of 178 questionnaires and 42 interview records. Occupational origin was defined as the "principal occupation of the respondent's father." To facilitate quantative analysis, a numerical value for occupational origin was obtained by scoring the father's occupation on the North-Hatt (1947) scale of occupational prestige The mean occupational origin of the 220 respondents was 77.7 points on the 100-point scale. For purposes of comparison, it may be noted that the mean occupational prestige of all male workers in the U. S. in 1925 is estimated at 61.0 North-Hatt points. These figure indicate that the occupational origin of the average business executive of today is considerably higher than that of the average gainfully employed male.

There were no significant differences in occupational origins of respondents between the four cities or the two geographicial regions. The means for the Northeast and Midwest samples were 77.3 and 78.2, respectively. The corresponding standard deviations were 6.55 and 6.70. The interview returns yielded occupational-origin means which were significantly lower than the questionnaire means, and it is estimated that if interview data had been obtained in the Midwest as well as in the Northeast, the regional means would have been approximately 77 North-Hatt points in each instance.

OCCUPATIONAL ORIGINS BY BUSINESS SIZE

Table 1 shows the relationship between size of business, measured by number of persons employed, and the occupational-origin scores of the respondents. The businesses have been grouped arbitrarily into size categories on the basis of inspection of the scatterplot of the two variables on a semilogarithmic graph.

Several points in table 1 are worthy of note. First, the distribution approaches the normal curve, with the highest occupational origins occuring among leaders of businesses in the 500-1000 employees range. Second, the range of recruitment, as indicated by the standard deviation of the origin scores, is sharply restricted in the

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middle portion of the distribution and widely dispersed on both ends. Third, the means of the extreme groups are significantly lower than the means of Group IV.

The configuration of the means curve is affected only slightly by the bias in the questionnaire returns. If the interview returns are weighted to compensate for their underrepresentation in the Northeast sample, the principal result is a depression of the ends of the curve. The center of the distribution remains virtually unaffected. This result reflects the fact that the mailed returns were biased in the direction of respondents of higher occupational origins.

In general, the data in table 1 appear to indicate that business leaders vary significantly in occupational origin when compared across business-size categories. The lowest origins are found in the leaders of the largest businesses, while the highest origins are found among owners or executives of middle-sized concerns. Leaders of the smaller businesses tend to come from approximately the same occupational origins, in terms of North-Hatt scores, as those in the largest businesses There are, however, some differences between the two latter groups in terms of religious affiliation, nationality of parents, and political party.

TABLE 1

Relationship between size of business and occupational origins of business leaders

Group	Number of Employees	Number of Business Leaders	Mean North-Hatt Rating of Fathers' Occupations	Standard Deviation of Mean North-Hatt Rating
I	100–149	72	76.4	7.5
II	150–299	47	77.0	9.7
III	300–499	38	77.7	6.0
IV	500–999	30	82.1	4.6
V	1000–4999	26	79.1	6.1
VI	5000–30000	7	72.8	10.9

A hypothesis suggested by these data is that the criteria of business-leader selection vary quantitatively and also qualitatively with business size. In particular, competitive behavior appears to control admission to executive positions more effectively at the lower and upper extremes of the range examined here. Entry into one extreme rather than the other appears to be largely a matter of possession of more or less of acumen, experience, or drive. The criteria of entry into the middle-sized businesses appear to be more stringent, possibly because of the presence of qualitatively different factors. Entrance into the leadership of these concerns may be based less upon open competition and more upon the meeting of traditional standards such as group membership or lineage.

CHARACTERISTICS OF THE BUSINESSES

Inspection of the characteristics of the businesses in Group 1 and 11 reinforces the suggestion that membership in these groups is the outcome of intensive competition. One evidence is the relatively large percentage of high-risk industries and businesses such as textiles, clothing, plastics, novelties and the like. Another is the relatively great heterogeneity of parental nativity, political affiliation and religious affiliation among the respondents in these businesses. The latter suggests recruitment from a wide group of potential members, while the former indicates a need for continual struggle to remain within the group.

At the upper end of the size range, the respondents are executives of well-established corporations or regional branches of national enterprises. The mobility pattern is one of having risen through the concern, or of having been brought in from another business of a similar character. The process, like that for

the smaller business leaders, connotes success in a competitive situation, since the present position appears to have been won on the basis of demonstrated ability. At the same time the criteria of selection appear to have been more standardized. There is greater homogeneity of parental nationality and of political and religious affiliation in the two groups than in the two lower.

The businesses in Group V and VI are for the most part capital goods or heavy industries, manufacture of machinery, electrical equipment, the processing and fabrication of metals, and engineering and construction services. The businesses in Group IV are essentially like those in V and VI.

Ownership of business is most common among respondents in Group I, with Group IV next in order of frequency. No business owners are present in Groups V and VI. The higher percentage of owners among the respondents in Group IV as compared with II and III suggest that the middle-sized businesses may employ lineage as a selection criterion more extensively than the contiguous groups. This would help to explain the higher occupational origins in this group. It should be observed, however, that the percentage differences in ownership between Group IV and the two groups preceding are not statistically significant.

SIGNIFICANCE FOR RECRUITMENT TRENDS

The pattern of mobility shown in the foregoing data appears to have meaning for the recruitment of business executives in future decades. The significance lies in the apparent relationship between these mobility differentials and several dynamic tendencies in contemporary economic life. This significance can perhaps best be explored in relation to three generalizations, namely:

(1) The practices which govern the selection of executives in the largest businesses are tending to become more widespread in this society.
(2) Businesses in the middle-sized group are becoming a smaller proportion of the economy.
(3) There is a continuing tendency for business organizations to shift from individual to corporate control.

Since the practical significance of these generalizations rest upon their validity, their status in current economic thought is a matter of interest. It is impossible to consider this point in detail, but some references to the pertinent evidence and its implications for executive selection can be made here.

Trends in executive selection procedures. Regarding the first generalization, the diffusion of recruitment criteria and procedures characteristic of large business seems assured in view of the dynamics of the process- the drive toward rationalization, i.e., increasing the efficiency of the economic organization. Particularly relevant here is the growing use of objective criteria for selection of individuals to head large business concerns. The broad movement for the study of leadership in business and industry (Fortune, 1950), and even the practice of subjecting wives of prospective executives to scrutiny (Whyte, 1952) illustrate this tendency.

The rationalization process has produced two general policies which objectify succession to business leadership (Drucker, 1949). One of these is the increasing practice of moving "staff" people to top management positions, thus availing the concern of experience gained in long years of service in a succession of administrative positions. The other is the growing tendency toward the development of "crown princes," promising young men who are selected and trained from the beginning for eventual leadership roles.

Illustrations of these and related tendencies are commonplace. The head of Grace and Company, in discussing recruiting practices, reports that his concern has stopped the "habit" of hiring "rich men's sons from swanky colleges" in favor of "hungry, brainy young men who are eager to knock themselves out" (Time, 1952). Similarly, the president of Bethlehem Steel states that one policy of his company

"prohibits the sons of executive officers from working for the company" (David, 1953).

Not all these "hungry, brainy" men will achieve the position of principal executive in their organization. Yet their presence in the organization indicates a shifting pattern of thought regarding leader succession. The changed climate alone would encourage the progression of some able men to top positions despite low occupational origins. In addition, the new recruitment policies facilitate upward mobility in the larger concerns by placing relatively more such men in strategic positions, and giving them familiarity with the expected behaviors.

Trends in business size. The generalization regarding the declining proportion of business in the intermediate categories is more difficult to substantiate. It may be noted that since the classic study by Berle and Means (1933) there has been wide acceptance of the belief that business concentration is continuing in this society. This belief has been strengthend by the disclosures of the Temporary National Economic Committee (1941) and the Federal Trade Commission (1947).

The significance of these findings becomes apparent when they are considered in relation to other data. Slichter (1948) observes that the average business firm has about the same number of employees today as in 1900. In addition, he points out that for the last four decades the number of non-agricultural business concerns has been increasing faster than the population. If there is simultaneously a tendency toward concentration, a maintenance of the same number of employees in the average concern, and an increase in the number of businesses, then there is a definite possibility that intermediate businesses are diminishing relative to small and large businesses.

This possibility has been described as actuality by Galbraith (1952) in the case of particular industries. He points out that the number of businesses tend to reach its maximum in a new field within a few years of inital opening up of the area. After that, there is likely to be a steady decline in number, stabilizing around a "handful of massive survivors, and usually a fringe of smaller hangers-on." Explanations of this process by failure to develop an effective managerial organization in many intermediate firms, or in terms of the high costs of management in these firms have been advanced by Gardner (1949) and Drucker (1949).

The relevance of an increase in the number of larger businesses at the expense of intermediate businesses is that it places a greater proportion of executive positions in locations where they are likely to be filled by persons chosen without regard to origin. The positions shift, in other words, into an area of the social structure where selection is more rational and impersonal. The role of ascribed status diminishes, and the role of achieved status increases proportionately in the recruitment of leaders to fill these positions.

Trends in business ownership. The decline of individual ownership of the larger and intermediate businesses is a well-established fact in this society (Berle, 1952). Its significance for the recruitment of business executives is that it too produces modifications in selection procedures. It encourages a tendency toward objective selection, focusses primarily upon the qualities pertinent to effective management of the enterprise and to the securing of profits. Because it is the largest businesses which are the most likely to pass out of one-family ownership, this tendency should be noted earlier and more clearly in the larger businesses.

The extent to which the tendency toward corporate ownership is a continuing one in this society is conjectural. Whatever its future course, its past effect appears to have been the shifting of the locus of the highest occupational origins among business executives from the larger to the intermediate businesses.

SUMMARY AND CONCLUSIONS

A study of 220 business leaders, sampled by mailed questionnaire and by subsequent interview of a fraction of the non-respondents, showed significant

variation in occupational origin of respondents in businesses of different size categories. The lowest mean origin was found among leaders of the largest businesses. Next lowest were those in the smallest-size category. The highest origins were found in businesses of intermediate size.

The trend in origin means for the several groups suggests that rational criteria and competitive selection procedures are most pronounced in the selection of leaders for the larger and smaller businesses. Traditionalistic criteria appear to govern most effectively in the intermediate businesses.

The observed mobility differentials may be interpreted as indicating that occupational origins of business leaders have declined in recent decades and will continue to decline in the future. This inference is supported by (1) the belief that objective leader-selection practices are likely to diffuse in this society, (2) an apparent decline in relative numbers of businesses in the traditional-criterion group, and (3) a possible continuation of the shift toward corporate ownership of business. Each of these tendencies appears to increase the likelihood that achieved rather than ascribed statuses will be the focus of attention in the recruitment process.

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Most books on the mosses have been written for specialists interested in the Bryophytes, one of the great divisions of the plant kingdom. These may be used as texts but ordinarily, students need the assistance of an instructor to successfully learn to use them. Dr. Bodenberg has succeeded in preparing a book on mosses which will appeal to nature lovers; to students who wish to become acquainted with this group of plants upon their own initiative; and it may be used as a text in Local Flora courses. In addition, the book will be useful as collateral reading for General Botany students. The chapter titles are as follows: What are Mosses?; The Place of Mosses in Nature; How to Study Mosses; Moss Morphology, a Description of the Parts of the Moss Plant; When and Where to Find the Common Mosses; How the Specialist Classifies Mosses; and How to Identify the Common Mosses. The last chapter is a field key to 27 moss families and 156 species found in the U.S.A.

GLENN W. BLAYDES.

TERRACE INTERPRETATION IN SOUTHEASTERN OHIO

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The terraces along the Ohio, Muskingum, Hocking, and Scioto rivers have attracted agricultural and physiographic interest for many years and have elicited several papers. It is believed that they can make a contribution to the glacial as well as to the river history of Ohio. To this end the author added to his previous studies extending over years of investigation a complete journey along these four rivers in the summer of 1953 from East Liverpool to Portsmouth on the Ohio, up the Muskingum to Zanesville, down the Hocking from Lancaster, and up the Scioto to Columbus. These terraces are not studied here as terrace patterns in the manner that terraces were studied by several able students at the turn of the century but rather as materials related to the several ice advances and to stream work.

Many authors in their reports by counties, by areas and by topics in the Ohio Geological Survey both of the Third and the Fourth Series have mentioned and often described terraces along these through streams in unglaciated Ohio. There are very few terraces along streams that do not reach back into glaciated Ohio, and none of glacial outwash or valley train material. How could there be outwash in valleys that never headed near the ice margins?

As has been known for many years, all four rivers have suffered modification as recently as in the glacial period. The narrow valley on the Ohio from Sardis, Ohio, to St. Marys, W. Va., indicates that two rivers once flowed in opposite directions from this section. The absence of any large tributaries in this vicinity also points to this as a divide area. The narrow valley from Duncan Falls to below McConnellsville on the Muskingum suggests a similar situation on this river. Likewise, the narrow place from the Athens-Washington County line north to Frost, and again below Haydenville on the Hocking indicate that streams, formerly flowing in different directions, were connected to make up this through river. The Scioto has probably been reversed from Sciotoville at the mouth of the Little Scioto River nearly to Columbus. These four changes will be reviewed later in this paper each under its own river.

The terraces are mostly of gravel and sand, are both high and low, some over 1,000 ft. above sea level (350 ft. above the river); the lowest just above river level, are mostly of gravel and sand. Some are of local fallen material or bed rock in place, others of rock covered with gravel and sand. The detrital material containing varying proportions of crystalline pebbles evidences glaciers from a Canadian source as one of the transporting agents. Except in the lowest terraces, which are flood-plain remnants and contain relatively little in the way of crystalline pebbles, the fragmental material of the terraces is interpreted to be glacial outwash. Inasmuch as the outwash displays various stages of weathering it is believed to have reached its present lodgment at different times and to have been exposed to weathering for different durations.

THE OHIO RIVER

That the Ohio River is a composite river has long been recognized. Old divides have been recognized near Cincinnati, below Cincinnati in the Kentucky-Indiana portion, at several places between Portsmouth and Marietta and again near Sardis. Other modifications occurred farther upstream in Pennsylvania. These modifications were not all accomplished at the same time but are ascribed,

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some to Teays and Deep Stage time, others to pre-Illinoian glaciation time and to Illinoian and Wisconsin times Stout and Lamb, 1938. (p. 80).

The Ohio Narrows. The long reach or gorge section of Ohio River is a nearly straight, narrow valley from St. Marys to New Martinsville, (fig. 1) two towns in West Virginia. This portion has been interpreted as a gorge, and its youthful appearance ascribed to the recency of the coming of the river through this part. It has been held by Stout and Lamb (1938) that Ohio River did not transgress this col in pre-Illinoian time, but that Illinoian ice forced water over the col. They also believed when they wrote that ice on the Ohio near Ripley midway between Cincinnati and Portsmouth, obstructed the westward outlet (Cincinnati River) and set water back up Teays, over Sardis area, and on northeastward toward the Atlantic. This of course occurred after Sardis col had been cut out by some previous transgression. Ireland (1940, 1943) finds crystalline pebbles and boulders high on hills in southeastern Ohio, pre-Illinoian outwash in valleys, and drift known in Western Pennsylvania that are all equivalent in weathering and erosion to Jerseyan (Nebraskan) rather than Kansan. He says with Leverett (1926, 1939) that Pennsylvanian drainage at this time went southward through the Sardis-New Martinsville gorge section.

Inspection in the field and a study of the topographic maps eliminate most of this "gorge" section as the exact site of the former divide. One mile above New Metamoras the 1,000-foot contour line lies on the bluff ¼ mile from the flood plain on the West Virginia side, and 920-foot line (top line on map) is ½ mile from the flood plain on the Ohio side. The two strips of flood plain and river combined are less than ½ mile wide; hence the bluff summits are only about one mile apart at this place. About 2 miles south of Sardis on the Ohio side the highest contour is 1,200 ft. and ¼ mile distant from the flood plain and on the West Virginia side is 1,160 ft. and ⅓ mile from the flood plain. The river and flood plain total just over ¾ mile; hence the bluff summits here, while a little higher than near New Metamoras, are 30–35 percent farther apart. Inasmuch as the New Metamoras "pinch" is in a narrower gorge section we are inclined to think that the transgressed col was at this place rather than near Sardis; but the ambiguity suggests a capture by head erosion (headward or headstream erosion) rather than a simple "push over" by glacial waters.

Looking for other possible similar cols over which the waters might have been forced, we find that the Wetzel-Tyler county line (fig. 1) is laid for many miles along a divide east of the Ohio River, starting near the river and extending southeastward with an altitude of about 1,000 ft. It rarely falls even a little below. This divide lies between tributaries of Fishing Creek and Middle Island Creek.

On the Ohio side of the Ohio River is a divide ridge between the tributaries of the Little Muskingum and Sunfish rivers that is about 1,200 ft. above sea level at Woodsfield, and does not depart far from that altitude. These divides probably have been lowered a little since the beginning of the ice age, but they must have been higher than the col near New Metamoras when it was first transgressed, else they would have been crossed instead. The Little Muskingum and Sunfish are in much more mature valleys than the present Ohio, especially near its narrow places, and Middle Island and Fishing creeks have very meandering courses in equally mature valleys. No doubt these four have matured some since the Ohio diversion, while the Ohio Valley has been touched up, much widened in places, to satisfy the needs of a larger stream than those in it before the diversion. When the ice-ponding occurred water went over the New Metamoras col because it was a little lower than any of the others; no matter whether the diversion was due to ice ponding or to earlier stream capture.

Terraces in the Ohio Valley. Terraces are found along the Ohio River from its beginning at Pittsburgh throughout its whole course. We shall examine only those in Ohio and above Portsmouth. There are many on the opposite side in

West Virginia and in Kentucky. No continuous bench can be traced for a long distance, but patches of terrace, more or less intact and nearly level-topped, are constantly in sight. The terraces are at various altitudes from over 1000 ft. above sea level down to stream level. From Beaver River south to New Martins-

FIGURE 1. Map, Ohio River from Pennsylvania line to Marietta with counties and towns.

ville, all but the highest descend with the present stream, the upper detrital ones more rapidly. The highest terrace series is of rock, free from outwash, and descends northward. Upper gravel ones are generally more deeply and severely

weathered and are more dissected. The lower ones approach the present flood plain, both in altitude and in nature of materials; as the river continues to cut down and lower its grade, remnants of the existing flood plain will be preserved and will then be counted as terraces.

Gravel-covered Terraces. The highest gravel and sand terraces on the Ohio River now occur over 900 ft. above sea level from East End above East Liverpool to Toronto in Jefferson County. At the latter place they are about 950 ft. They are primarily of bed rock, sometimes called gradation plains (Chamberlin and Leverett 1894) and are more or less covered with gravel or sand on top. The terrace top falls gently southward. They may be seen up the slope back of Vulcan on both sides of the little run and back of Wellsville a half mile north of McQueen Run. The continued presence of crystalline pebbles, granite, gneiss, quartzite, and schist of Canadian origin, shows that the material is certainly outwash from a glacier or from a moraine or till sheet. Its much weathered condition means that it came from very early glaciation, Stout says, Nebraskan, (Jerseyan) and the author concurs. It is far older than known Illinoian gravels. While the terrace top falls southward from place to place, the rock terrace below the gravel falls northward. These descents indicate that the rock terraces were made by a north-flowing stream before the diversion; and the gravel, falling southward, was laid by a south-flowing stream, hence after the diversion. Since the terrace material is old enough to be called Nebraskan and lies in a valley made before the gravels came, the valley over the col at New Metamoras must have been opened not later than Nebraskan time.

Leverett (1903 p. 88) furnishes valuable light on this problem by pointing out many rock terraces higher than the gravel-topped ones that descend northward along the river from Moundsville, W. Va. to the present mouth of Beaver River, Pa., and others less frequent 10 to 12 miles south of Moundsville. These suggest that the reversal of drainage here may have been by capture (headward erosion); that a south-flowing stream etched northward foot by foot and offered the north-flowing stream an easier grade southward.

If the col is placed near New Metamoras, as suggested earlier, the capture began there. A field or topographic map study shows that south from here the tributary streams enter the Ohio pointing southward, while upstream many enter pointing northward.

The col was cut before Nebraskan time for the gravel-train of very old Nebraskan (Leverett 1939) gravel is found near Chester, West Virginia, opposite East Liverpool at 1000± feet and at 980 ± at Bellaire. Stream capture is not an unknown process in southeastern Ohio (Leverett 1939; Merrill 1953). This interpretation would give a lower divide on the Ohio River than on any other in southeastern Ohio in Nebraskan time and would explain why the Ohio is the only valley having such old terraces.

Lower terraces are more frequent than high ones on the Ohio. One of these lower terraces can be seen at East End, a suburb just east of the town of East Liverpool. It consists of old weathered glacial gravel and sand, many crystalline pebbles among local (Ohio or Pennsylvania) material none of which is fresh. Cisterns and cellars dug in the terrace do not reach rock. Thickness of the outwash fill is reported to be 15 to 30 ft., and its surface is about 750 ft. above sea level. This material is distinctly older as shown by deep weathering and more weathering than such deposits classed as Illinoian, but not as old as the higher ones just described. It may be evidence of Kansan glaciation to the north. At Wellsville is a similar terrace. In places this material seems more like till, but the weathered sand and gravel constitute most of the terrace.

On the Virginia side, across the river and downstream one to two miles, a great terrace spreads in two levels. The northern portion is about 740 and the southern 760 ft. above sea level. The stream here is below 660 ft. for the 660 contour line crosses at East Liverpool.

Beginning over two miles below Sardis and extending more than six miles along the river stretches a terrace of gravel and sand. A pit opened in this terrace (fig. 2) has a fresh face of 35 ft.; the upper third is yellow sand; lower two thirds is poor weathered gravel. Some fragments of local rock are 3–4 ft. through. Locally, gravel is partly cemented with lime carbonate; but the weathering is far better evidence than is cementation that it is probably an Illinoian terrace.

At New Metamoras, at Grandview, and at Reno near Marietta, are old weathered gravel terraces. Some are roughened by erosion. The terrace at Reno and at Evergreen Motel at Shade, a mile above Marietta, is 7 to 8 miles long, only about 20 to 40 ft. above the present flood plain, and consists of the same old gravel, apparently of Illinoian age. Rock below is not to be seen. Presumably much of the upper part of this terrace has been eroded away. It is a carved terrace of older filling. When the glacier, whose waste is here, came to Ohio, this valley must have been as deep as it is now.

FIGURE 2. Gravel pit in terrace about 3 miles below Sardis, Ohio; upper 10–12 feet is yellow sand, see top bench cut back; lower nearer part is weathered gravel.

Near a place called Gravel Bank a few miles below Marietta, a terrace ½ to 1 mile wide extends 3 to 4 miles along the Ohio River (Ohio side) about 20 ft. above the river (615, 617, ft. above sea level). The terrace has yielded abundant commercial gravel since 1910. While this gravel is well supplied with crystalline pebbles, hence is reworked glacial drift, it may be recent alluvium, really a flood-plain terrace. It is not much weathered in place.

The next down-stream terrace upon which Belpre and Belpre Center have been built, is over 650 ft. above sea level and consists of old weathered outwash material, very sandy at the top where the terrace is well dissected. This is much like the terrace and material found two miles below Sardis but not so bouldery.

Long Bottom is a terrace just above flood level, and while its gravel is rich in crystalline pebbles it is believed to be a modern flood-plain area. Its non-crystalline pebbles are very fresh fragments.

A terrace extending about two miles each side of Portland (fig. 3) is dissected and rises strongly toward the bluffs where it is 620 to 680 ft. above sea level.

The river here is about 550. Material and form, as well as position, indicate this to be a flood-plain remnant. Buffington Island, although 40 ft. above the water, is part of the flood plain. These are mentioned to show the character of the flood plain and to assist in the interpretation of the higher terraces.

At Gallipolis and upstream beyond Kanauga ls a terrace of fresh, recent Wisconsin outwash, whose front is cut into two, and in places, three steps. The Home for Epileptics is on the upper one, which is 100 ft. above the river level.

At South Point, 10 miles above Ironton, the gravel terrace has not been opened commercially, but it seems to be Wisconsin outwash. Ironton spreads over a similar sand-gravel terrace more than 40 ft. high. Down stream a few miles is a larger terrace rising from 540 ft. near the river to 560 near the bluff.

FIGURE 3. Map, Ohio River from Hockingport to below Portsmouth with counties and towns.

River level is about 475 ft. The terrace is gravel with yellow sand on top and has an open gravel pit about a mile from Haverhill. This is believed to be a Wisconsin terrace because of its height and the sand layer on top. Crystalline pebbles are very rare. All tributary streams from here up to Muskingum and Hocking rivers head in unglaciated territory and would add no crystalline material. Thus Ohio waste greatly predominates.

THE MUSKINGUM RIVER

This river heads in many tributaries above Coshocton (Mohican, Tuscarawas, Kokossing) and receives the Licking at Zanesville. Before the Ice Age its waters made their way westward from Coshocton, Muskingum, and other counties through the old Newark Valley, old Cambridge and Groveport valleys to the large Teays River which led westward to and across Indiana and into Illinois (Stout *et al.*, 1943).

The Muskingum Narrows. There seems to be no question but that the Muskingum valley, as interpreted years ago, is made up of two valleys whose

streams headed almost exactly where the Morgan-Muskingum county line comes or, in other words, near Cedar Run 2 to 3 miles south of Blue Rock (fig. 4).

Terraces in Muskingum Valley. Along the Muskingum, where there has been much landsliding, the terrace material often contains masses of waste and fresh rock from the young bluffs. For this reason some of the terraces resemble moraine in form but not in materials. These forms are also distinguishable in some places by the scar on the bluffs from which the waste fell.

As shown above the transgressed col in Muskingum Valley is at Muskingum-Morgan county line. From a mile above Rokely Lock to a mile below is a terrace 40 ft. above the stream and about 700 ft. above sea level. Its glacial gravels are

FIGURE 4. Map, Muskingum and Hocking rivers with counties and towns.

being excavated commercially but they are badly weathered and are as old as Illinoian, possibly Kansan. Hence the col just above, at Blue Rock, was transgressed before the Illinoian glacier came, probably initiated by the Kansan or Nebraskan ice sheet. Another terrace of old glacial gravel occurs between Blue Rock and Duncan Falls. Above Duncan Falls and extending nearly to Zanesville is a large gravel terrace, a trifle higher than those down stream. It has been carved into two steps in places and into three in others. A commercial gravel pit has been opened about midway in it, revealing its glacial and badly weathered character.

These terraces, descending gently down stream a little more steeply than the present stream, were laid after the col was cut through and date the cut at least to a pre-Illinoian time. Some seem as old as the oldest on the Ohio River.

At Stockport and McConnellsville, ten miles above Beverly and just above Hooksburg, are extensive gravel terraces mostly less weathered and hence younger than those above described. Several are commercially opened, and the Stockport terrace is carved into two steps about 700 and 733 ft. above sea level. These are classed as Wisconsin. They are far less weathered than the older ones. An example of the very old gravels on Muskingum was found near Lock No. 2, about

4 miles above Marietta. It consists of old gravel and sand, mostly pebbles of granite, gneiss, schist, quartz, and quartzite, often much weathered. There is little Ohio rock recognizable in this terrace at present. At Lakeside Motel just west of the mouth of Sugar Run are similarly weathered, old gravels in the terrace. This terrace is said to rest on limestone. Little ledges can be seen low on the face or front of the terrace.

To sum up, there are terraces on the Muskingum of at least three ages, Wisconsin, Illinoian, and an older stage, probably Kansan. These are all above the present flood-plain terraces. The diversion of water over the col below Blue Rock must have been early enough to permit the new through-stream to carry Kansan outwash and lay it along the valley. There seems no way to invoke headward erosion and piracy, as in the case of the Ohio River, but neither is there any way to prove that the diversion or capture was not done by headward erosion that left no obvious evidences, such as are preserved along the Ohio. The author thinks very early glaciation was the agent that effected the union of two streams to make up the Muskingum.

THE HOCKING RIVER

The Hocking River came into existence during the ice age. A divide extended NE—SW across Hocking, Perry, Morgan, and Muskingum counties separating NW flowing small streams headed for the Groveport River (Stout, *et al.*, 1943) from south-flowing streams headed for the Marietta River and the Teays. Most of these south-flowing streams have been named (Stout, *et al.*, 1943). Hamden started in Hocking County, was joined on the east by Zaleski near McArthur in Vinton County, and entered the old Marietta River and through it the Teays. East of Hamden was Albany River formed by Licking and Chauncey creeks from Perry and Athens counties and flowing across western Meigs into Marietta River in Gallia County. A third unnamed crossed eastern Athens County, and the fourth, Barlow Creek, gathered its waters in Morgan County, and crossed Washington County into Marietta River, very near where the present Hocking joins the Ohio (Stout, *et al.*, 1943).

Hocking Narrows. This arrangement of old drainage accounts for the failure of Merrill (1953) to find evidence of the Teays stage in the Hocking valley. The author has not followed any of these old streams southward in the current terrace study but has seen the divides between them now crossed by the Hocking. The two most notable (Tight, 1903) are the one (Merrill, 1953) east of Haydenville called by the early workers the Nelsonville divide or col, and the one near the village of Frost (fig. 5). The former has been carefully studied by Merrill; the latter has a very narrow valley across it and the bluffs attain their maximum height (800–850 ft.) within a half mile of the stream. Thus the old stream leading to the Ohio (Marietta probably) was only about 8 miles long.

Another narrow place in the Hocking valley is above Logan between Rockbridge and Enterprise. In this area an abandoned valley lies west of the present Hocking course and is filled over 100 ft. deep with outwash. Drainage from the west comes down into this valley, and Buck Run brings part of it out to the Hocking at Rockbridge. Clear Fork brings the rest out farther south entering the Hocking near Logan. No drift is known over the immediate hills in this vicinity. Outwash may have been sent down the valley sufficient to aggrade this abandoned valley to the level of low divides in the present course. This aggradation would send water over the divides until a valley was made lower than the aggraded abandoned valley. Such diversion must have occurred long ago, for the outwash in the abandoned valley is weathered more than known Illinoian, and the current valley is already becoming mature. Merrill (1953) notes Illinoian outwash in several places near and infers that the drainage changes are pre-Illinoian. This author would concur.

Terraces in the Hocking Valley. Leverett makes the point that the Hocking carried much Wisconsin outwash, relatively more than either of the streams so far considered; at least relatively more is preserved. Clear Creek, a tributary that heads farther west in glaciated territory, comes through a gorge from the west and enters the Hocking between Sugar Grove and Rockbridge. Terraces of Illinoian outwash are below the gorge, not along Hocking, but just off Hocking in Clear Creek Valley. They were made after Clear Creek had been forced over the col at its gorge section and when Hocking provided an outlet for it southeastward; hence the Hocking col transgression below Frost must have dated from about the same time, pre-Illinoian.

In the abandoned valley from Rockbridge nearly to Logan, now drained southeastward by Clear Fork, are quantities of Illinoian outwash. The valley is much more mature than the valley now occupied by the Hocking beside it. This modification is pre-Illinoian. Kansas or Nebraskan ice probably came near enough to block the northward flow of the Hocking waters here. Merrill (1953) concurs; others say it is Wisconsin (Stout and Lamb, 1938; Stout *et al.*, 1943). How could it be a Wisconsin diversion with Illinoian or older outwash in it?

FIGURE 5. Narrows on Hocking, looking down stream from bridge near Frost.

Wisconsin outwash is found in the terraces upon which Logan, Nelsonville, and Athens stand, but upper terraces here as elsewhere are Illinoian. At Enterprise the new road, Route 33, cuts through a terrace 100 ft. above the flood plain. Houses formerly upon it have been removed and a big cut for commercial gravel made. The gravel is dirty, not well sorted, gravel from sand, and carries pebbles up to 8–10 in. in diameter. A layer of fine sand 10–15 ft. thick is on top. There is some cementing and very little weathering.

Another large Wisconsin terrace has been opened between Lancaster and Sugar Grove on the southwest side. The lower half of the gravel is cemented with calcium carbonate. Three miles below Logan, east of the road, is a hill shown on the topographic map to be 220 ft. above the river. It is a remnant of a terrace and has been opened for gravel. It has pebbles of Columbus limestone and many Ohio rocks as well as a wide range of crystalline rocks, shows very little weathering, and is cemented in the lower 25 ft.

From the bridge near Beebe on down below Frost, both villages in Athens County, are several remnants of Wisconsin gravel terrace. Our findings confirm Leverett's point of much Wisconsin outwash in Hocking Valley (Leverett, 1903,

1926) and establish the Hocking stream adjustments as pre-Illinoian with abundant outwash terraces of both stages.

THE SCIOTO RIVER

The Scioto River gathers waters far north in Hardin and Marion counties and flows south across Delaware and Franklin counties. The Olentangy gathers about as far north from Marion and Morrow counties and flows south near the Scioto which it joins in Franklin County at Columbus. The Scioto thus greatly enlarged continues on southward in a broad, open rural valley to the Ohio River in the western part of Portsmouth, passing enroute Circleville, Chillicothe, Waverly, and Lucasville.

Scioto Valley. The Scioto Valley has no narrows as have the others heretofore discussed, but always has plenty of room for its stream with its broad meanders. Its source rivers head far back in glaciated Ohio, for the ice advanced farther south than Circleville over its present head-water area. It has often received not only meltwater from the ice but great quantities of outwash material.

Extended studies by earlier workers showed that the waters flowed northward and have been reversed from Portsmouth about to Franklin County. That the Teays in pre-glacial time flowed from Kentucky into Ohio, in eastern Scioto County, and that the various turns well known in Jackson, Pike, and Ross counties brought waters from the Old Appalachians, the New Appalachians, and the Cumberland Plateau to flow northward in the Scioto Valley through Pike, Ross, and Pickaway counties, then northwestward through Union, Champaign, Shelby and Mercer counties has been gradually worked out. A small Scioto called Portsmouth River flowed northward from the Ohio near Portsmouth to join the great Teays River in Pike County. (Hyde, 1921; Lamborn, 1932; Leverett, 1903, 1926, 1942; Mather, 1909; Stout and Lamb, 1938; Stout *et al.*, 1943; Tight, 1897, 1903).

The reversal of this small Portsmouth River with the part of the Teays that occupied part of the present Scioto Valley has often been noted. The upper Scioto and Olentangy rivers are in almost purely postglacial valleys and are flowing on bedrock almost all their courses. When the reversal came, the Portsmouth offered an easier route to the developing Ohio toward the west than did the Teays; hence that was the route chosen instead of any other, even though it meant cutting out a divide in one or two places on the Ohio below Portsmouth. Thus the Scioto route was laid out for the movement and deposition of outwash.

Terraces in the Scioto Valley. The terraces in the Scioto Valley are of several kinds. A series of rock terraces with glacial gravel caps is described by Leverett (1903), and they are still there. Near Chillicothe the terrace cap stands about 100 ft. above the river and 700 ft. above sea level. The rock terrace is about 600 ft. high. Near the Pike-Scioto County line, about 30 miles south, a similar terrace is known. The gravel top is here 650 ft. above sea level and the rock terrace below it is at 625 ft. Thus the gravel terrace falls southward about 50 ft. in 30 miles while the rock terrace falls northward about 25 ft. in the same distance. The gravelly outwash is about 100 ft. thick near Chillicothe and only 15 ft. at the mouth of the Scioto. The rock shelves are known at a number of intermediate points and on downstream.

This series of rock terraces is good evidence that the river which made it was a north-flowing stream. Topography and many other points are known to support this interpretation. The gravel is undoubtedly old. It has been traced to the Illinoian drift border, and is weathered amply to be Illinoian. If that is its status, the river that made the rock terraces was reversed before Illinoian time. The outwash at Chillicothe (Hyde, 1921; Leverett, 1942) extends below present river level, hence is over 100 ft. thick. A valley was thus carved below the rock terrace before Illinoian gravels were heaped on it. To have so deepened the valley before

Illinoian gravels came, the reversal of Scioto River flow must have been accomplished as early as Kansan time and probably by the Kansan or even Nebraskan ice sheet as it came in over northern Ohio and stopped north and northwest-flowing streams. The process must have been comparable with that disclosed in the upper Ohio and Muskingum valleys.

From Waverly down the Scioto, outwash gravels and terraces are rare, limited to small remnants, but the flood plain is over a mile broad. Thus it seems that if outwash was ever laid along the lower Scioto it has been almost completely removed. Even the flood plain rarely has crystalline pebbles. Weathering and corrosion have reduced them to clay, silt, and fine sand.

From Waverly up river to Higby, over 7 miles, there extends a great terrace of Wisconsin outwash. Its surface is 75 to 100 ft. above the flood plain and is somewhat roughened by small stream erosion, but usually overlaid with a layer of sand. Pebbles of crystalline and Ohio sedimentary rocks are fresh and frequent. The stream-cuts and a large active gravel pit made thorough examination possible. These lines of evidence point to its Wisconsin age, although Illinoian terraces are known nearby. (Hyde, 1921; Leverett, 1942)

Other Wisconsin terraces occur between Chillicothe and Circleville, but these are among the Wisconsin moraines and are all unweathered Wisconsin outwash. The river has certainly played havoc with the outwash deposits once laid in the valley which then corresponded in height with the Waverly-to-Higby remnant.

SUMMARY

The streams that have carved these river terraces in all four valleys are more or less meandering. In places they are quite systematic, but usually they simply wander from side to side planing away a little here and there, undercutting extensively at other places, and again flowing for miles without accomplishing any significant lateral work. This appears to have been their habit for ages, or at least since Illinoian glacial time, because their terraces are not systematic. Some show good form, such as cuspate fronts, divided scarps, and other regular stream-made terrace patterns; but as a rule they have quite the opposite appearance—long, straight fronts, or little notches, uneven steps, and unclassifiable patterns. Nowhere does there seem to be the wealth of systematic detail of pattern found in the Connecticut Valley or in its laterals as at Westfield, Massachusetts.

Correlation. Above current flood plains the materials of the terraces are almost universally of glacial origin, as shown by the abundance of pebbles from out-of-valley and even out-of-state Canadian crystallines.

The materials show differing degrees of weathering. The upper terraces and the materials next to the valley walls have suffered the most disintegration and thereby testify to the extensive duration of time since their placement.

These four streams reach far back into glaciated territory and most certainly carried drainage and waste directly from melting ice fronts and for longer time from areas mantled by drift where the ice lay and melted. We know from widely scattered places and many lines of evidence that the ice came more than once into the general area at northern central United States. Hence there might well be outwash gravels and alluvium of more than one age to account for the varying degrees of weathering and the eroded condition of the terraces.

Our glacialists have drift evidence of four advances (Jerseyan in Western Pennsylvania, Illinoian from Holmes County, southward and southwestward toward Cincinnati, and at least two stages, perhaps three, of Wisconsin age from Butler County north in western Ohio) (Desjardins, 1933; Ireland, 1940, 1943; Lamborn, 1932; Leverett, 1903; Stout *et al.*, 1943, 1953; Ver Steeg, 1931; White, 1931, 1937, 1939) of ice into the Ohio Valley, and from our terraces we can be just as sure of four ages of outwash, Nebraskan on the Ohio, Kansan on the Muskingum, Illinoian, and Wisconsin on all. We are not so far able to distinguish Early,

Middle, and Late Wisconsin terraces. There is one stream diversion, pre-Nebraskan, on the Ohio, probably by a headward erosion capture; a pre-Kansan diversion on Muskingum, probably caused by Nebraskan ice; and pre-Illinoian changes on Hocking and Scioto, probably caused by the Kansan ice sheet. On these four main streams there are no diversions of Illinoian or Wisconsin age. Such were all earlier, but changes on their tributaries can be traced to both later ice invasions. (Frye, 1940; Mather, 1909; Merrill, 1953; Stout and Lamb, 1938; Tight, 1900)

In making use of terraces to unravel river and glacial history it is reasonable to expect to find evidence of any glacial advance in the presence of terrace of that age. In like manner, any area of drift within our river basins may suggest terraces of the same age. Drainage modification attributable to any ice advance may be used as evidence of such advance. There should be no discrepancies or conflicts between evidence from these three sources. There is no doubt but all the several ice advances recorded in central North America were near here somewhere and perhaps advanced farther than we yet can prove. Certainly all the time passed over Ohio that is recorded anywhere else in Pleistocene of central North America. Even if no positive evidence of a glacial stage or of some interglacial interval has yet been found here, we still can bank on all the time here that is required for such events elsewhere.

Flood Plains. All flood plains may be carved into terraces, and all terraces, with the exception of the rock terraces, have been valley trains or flood plains. Even the rock terraces were at stream level at one time as are flood plains today. It might be better to say that the streams were once flowing on the level of the rock terraces. One statement is as true as the other.

In general, one may say a flood plain is a plain along a river but not too high to be subject to floods. Narrow valleys can not have wide flood plains. Wide valleys may have broad flood plains. The Scioto has the widest valley, but its flood plains are not nearly as extensive as they might be if the river should swing laterally enough to remove more of its outwash terraces.

The Scioto has much the largest valley among the four rivers considered in this paper. It has a more mature valley than any of the others. It has no constricted place as have the other three; hence it is believed never to have been modified by headward erosion or by having waters forced over a col between two streams flowing in opposite directions.

There is no place below Columbus where the flood plain of the Scioto is less than a mile wide; and there is no place in any of the other rivers in the section within the scope of this paper where the stream has a flood plain a mile wide. None of the other three rivers have as gentle grade as the Scioto. In the case of the Scioto it is worthwhile to think of the effects of tilting or diastrophic movements in its glacial history. The movements of the land downward as the ice came on and upward as it melted off are not great, only 2 or 3 ft. in a mile, and no doubt there were such movements in the ice-covered portions of Ohio. They were too small to be a factor in what has happened in these rivers, unless it be in the headward erosion in the Ohio. In the Scioto grades are so low and have been for so long that there is more relative chance there for the tilting to be a factor; but since there is no evidence of headward erosion captures in the Scioto, the tilting would only need to be considered in studying and comparing levels of terraces. The rock terraces descending northward, as described above, have a slope gentle enough to be appreciably modified by such tilting as is known to have occurred. It is believed, however, that the depression of the land by the oncoming ice was practically balanced by elevation when the ice melted off, so that consideration of such tilting may be unnecessary in making appraisals of any serious difference in the terrace levels as we find them today.

The author hopes that the above consideration of some angles of our terrace

problems may make a contribution to the study of glacial and river diversion problems.

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OHIO'S CONTRIBUTION TO METEOROLOGY, A BRIEF HISTORICAL RESUME

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Occasions such as this One-hundred-fiftieth Anniversary of Ohio University provide much needed cause to pause in our daily pursuits and renew our perspectives. I should like briefly to review with you the background structure of modern meteorology on this particular occasion because of two somewhat irrelevant but nonetheless interesting facts, i.e., (a) the science of meteorology has experienced practically all of its growth since Ohio University was founded and (b) Ohio and Ohioans had a particularly prominent part in the early development of meteorology in the United States.

In 1804, meteorology was still very much wrapped with the swaddling clothes in which Aristotle presented it to the world. Although he, in the fourth century B. C., strongly fostered the view that the weather was a physically, not a spiritually, controlled complex of phenomena, in 1804 weather was still something for which deities were blamed or praised, beseeched or propitiated by a large proportion of the earth's population.

The weather map with which we television viewers of America have become familiar in the last decade had not yet been invented one hundred and fifty years ago. Professor Heinrich Wilhelm Brandes of the University of Breslau constructed the first known series of daily weather charts about 1820, but the virtues of the synoptic map remained undeveloped for over thirty years.

A war, and a great naval catastrophe provided the impetus which was needed. In 1854 the French fleet, led by the battleship *Henri IV* was preparing to launch a massive attack upon Sevastopol when a violent storm struck the Black Sea, decimating the fleet and damaging the *Henri IV* very seriously. At about this time, M. U. J. J. Le Verrier of the Paris Astronomical Observatory had sprung suddenly into world prominence by correctly predicting, publicly, the existence and location of the planet Neptune. Emperor Napoleon III, judged that a scientist who could discover a new planet so beautifully should be a good man to devise the means for predicting the weather. As a result, Le Verrier was assigned this difficult problem. He assembled all of the data he could find in observatories and universities and, by plotting them synoptically on maps, showed *post facto* that the Black Sea storm had developed and moved regularly in time, so that a simple free hand extrapolation of the wind and pressure patterns would have predicted its arrival. This, to my mind, represents the beginning of modern meteorology, just about a century ago.

By definition, the synoptic method of Le Verrier requires that simultaneous observations from broadly distributed stations be assembled promptly at some point. If forecasts of the weather are to be made, the period between observation and forecast must be a minimum, and the obvious bottle neck is communication. For various well-known historical and practical reasons, therefore, it is not surprising that application of the method in the United States was delayed until 1868, and that then it was launched under the auspices of the Western Union Telegraph Company. It was the idea of Mr. Frank A. Armstrong, manager of the Cincinnati office of Western Union, to collect and publish daily the Weather reports from a number of cities. Soon after Mr. Armstrong started this pro-

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gram, Professor Cleveland Abbe of the Cincinnati Observatory recognized that these data could be used by the application of Le Verrier's method to make weather forecasts. He proceeded to enlist the support of the Cincinnati Chamber of Commerce and the cooperation of the Associated Press with a proposal to "—— enter these observations upon an appropriate manuscript chart—send the daily digest of the weather to the Associated Press—(and) accompany it with such general predictions of the weather for the next two days as—(the Cincinnati Observatory staff)—may seem authorized to venture upon." The proposal goes further by offering the daily digest and weather predictions to the AP and other cooperating institutions gratis.

On February 2, 1869, the first current weather map for the United States was issued for publication by Professor Abbe and Mr. Armstrong. Largely as a result of this effort, and that of Mr. I. A. Lapham of Milwaukee, the Congress enacted a law charging the Signal Service of the United States Army with the duty of providing national weather service. In the autumn of 1870 the weather map publication of Abbe and Armstrong was succeeded by the Tri-Daily Government Weather Map, and in 1871 Abbe joined the federal weather service. Thus after two years, the efforts of these two Cincinnatians led quite directly to the establishment of the first United States Weather Service.

Another prominent Ohioan, Dr. T. C. Mendenhall of the Ohio State University was also active in the promotion of weather science in this country. Through his efforts, combined with those of General W. B. Hazen, Chief Signal Officer, U. S. Army, a meteorological Bureau for the State of Ohio was established by act of the General Assembly in April, 1882. The Ohio Bureau, under the directorship of Professor Mendenhall, chairman, Mr. W. I. Chamberlain (State Board of Agriculture), and Mr. George H. Twiss, issued monthly reports for the state from October, 1882, to April, 1896, when all its functions were given over to the U. S. Weather Bureau.

Since 1896 Ohio has not been particularly prominent as a center for meteorological developments, although some important experiments have been conducted in the state. The Muskingum watershed study set up under WPA auspices and directed by Dr. C. W. Thornthwaite provided an unprecedented store of information on rainfall and flood patterns of that area. The thunderstorm research sponsored by the military and conducted at Wilmington, Ohio, during and following World War II yielded much new information about the processes and characteristics of thunderstorms. Unfortunately Ohio's part in these contributions was almost purely a matter of geography rather than talent.

At the present time a small program of teaching and research in meteorology has developed at the Ohio State University under the Department of Physics and Astronomy. We have awarded several degrees carrying a major in Meteorology, including among these three Master of Science Degrees and we are this year, announcing a curriculum leading to the Bachelor of Science Degree in Meteorology. The researches have ranged from cooperative projects with the Department of Zoology and Entomology and the Mapping and Charting Research Laboratory to relatively specialized problems within the fields of meteorology and physics. Among active research problems at present are the study of natural and artificial precipitation physics, the computation of the exchange of carbon dioxide between the atmosphere and the oceans, and the analysis of the changes of climate which have occurred within the period for which we have adequate records.

It does not seem likely that these studies will serve in the immediate future to distinguish Ohio particularly, but there is one field in which our state is definitely interested and in which she might again engage in a pioneering effort. I am referring to the practical application of modern weather modification and control techniques for the maximum benefit of the public.

ABORIGINAL CULTURE TRAITS AS REFLECTED IN 18TH CENTURY DELAWARE INDIAN TREE NAMES[1]

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In the Ohio Journal of Science (Mahr, 1953) the writer described a method of locating Indian localities on modern maps by means of analyzing a few 18th-century Delaware Indian place names as to their semantic components, and then checking the descriptions which they provided against the topography of the areas in question, as presented on the respective Quadrangle sheets of the U. S. Geological Survey Map.

Not only could these localities be identified beyond any reasonable doubt, but a much more significant result was obtained besides: it became evident that the principle which governs the compounding of these place names is a revealing expression of the Delaware's basic attitude toward their natural environment. Continued studies showed that this formative principle likewise underlies their names for plants, animals, and also inanimate objects.

As a fact of major significance it was learned that by far the majority of Delaware appellations of practically all sorts were dynamically functional, rather than statically descriptive, in character. Hence, they promised, upon semantic analysis, an abundant yield of first-hand clues to diverse aboriginal culture traits of the Delaware, or Lenni Lenape, Indians; at such detail, moreover, as hardly obtainable from any other sources.

This assertion will presently be confirmed by the semantic analysis of a few 18th-century Delaware Indian names for trees and tree products. The terms to be analyzed, as well as those used in substantiating their etymologies, have been taken from the Delaware column of David Zeisberger's Dictionary in Four Languages, compiled by him and some of his Moravian fellow-missioners, during the 1770's and 1780's, in the Tuscarawas Mission area of eastern Ohio. In 1887, the manuscript was published, without much editing, by E. N. Horsford, but has been out of print for many years. The four language columns, covering each of the 362 pages of the original manuscript in the Howard University Library, are, from left to right, English, German, Onondaga (which is Iroquoian), and Delaware (which is Algonquian). The main obstacle to this dictionary's previous use as a source for language and culture studies was found in the fact, brought out in the past by several critics, that Zeisberger and his Moravian helpers had listed the Delaware terms indiscriminately in either Unami or Munsee, the two main Delaware dialects, without ever indicating which was which. After having found out, however, how nevertheless those multiple-stem compounds can be separated and interpreted, and by drawing inferences by analogy, this writer eventually obtained workable results. A valuable clue to the procedure to be followed was offered by Zeisberger (1910), page 144, who states that "the dialect of the Munsee . . . is a key to many expressions of the Unami. The latter have a way of dropping some syllables, so that without a knowledge of the Munsee dialect it would be impossible either to spell certain Unami words or to guess their meaning. The Unami adopted many words from the Munsee, and the Munsee, from the Unami."

For the acquiring of practice in discriminating between the two dialects, Voegelin (1940) proved basically helpful.

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[1]Essentially, this is a paper read before The Ohio Academy of Science, Section of Anthropology and Sociology, at its annual meeting at Ohio University, Athens, Ohio, on April 16, 1954. The preparation of this article was supported in part from funds granted to Ohio State University by the Research Foundation at Ohio State University for aid in fundamental research.

Zeisberger's and other Moravians' spelling of Delaware terms, which is based on their native German phonology, has been transcribed, in these pages, into a more intelligible spelling mainly based on English usage; for example: *sch* has been changed into *sh*, *g* into *k*, *b* into *p*, *-eu* into *-ew*, *j* into *y;* while the vowels, *a*, *e*, *i*, *o*, *u*, also when duplicated for length, have retained their German sound values, the same applying to *ch*. Wherever *tch* occurs, it is the equivalent of *ch* as in Eng. *ch*urch. Zeisberger's *wu-*, or *we-* (*w*-plus sheva) is represented, in these pages, by *w'-*; similarly, *mu-*, or *me-*, by *m'-*. Where (') occurs, following any other consonant, or preceding a vowel, it has the sound value of a 'stop'.

These phonological approximations were adopted after a careful check against the sound conditions in Delaware dialects extant today, as presented by Voegelin (1940).

Before proceeding to analyze the names of specific trees, a few Delaware terms pertaining to the Forest and to some of its vital products will be examined as a typical demonstration of the principle governing the Delaware approach to the naming of things.

The Delaware term, in Zeisberger's *Dictionary*, for 'forest, woods', is *têkene*. Far from carrying any connotation of what *we* associate with 'forest', or the Germans, with *Wald*, *Busch*, namely a 'continuous area covered with trees', *têkene* denotes 'an uninhabited place', a definition listed, by way of explanation, by Brinton (1888). Only with the aid of this essential hint has it been possible to interpret *têkene* as a contraction, almost beyond recognition, of an older Munsee or early Unami form **ta/wiik/heen/e*, of the following composition: (*at*)*ta-*, negative prefix denoting 'no, not'; *wiik-*, stem with the meaning of 'structure'; *-heen*, 'to make'; and *-e*, suffix of place or time; adding up to a composite meaning: 'no building of houses here'. It indicates that the Delaware Indians did not build their dwellings in the forest proper but rather in open places near its fringes.

The stem, *wiik-*, denoting 'structure', is likewise present in *wiik/pi*, a Delaware term for 'tree bark'. Its remaining component, *-pi*, in whatever compound it may occur, signifies 'substance', or, more specifically, 'material to do it with'. Zeisberger's *Dictionary* carries the English definitions, 'bast', and 'inner bark of trees', while its German equivalent likewise is '*der Bast*'. In this connection it is significant that another English name for the Linden (*Tilia americana* L.) is 'Basswood' (*bass* for *bast*), indicating that Linden 'bast' was, and still is, preferred for some human uses to that of other trees. The Delaware, moreover, had a specific term for 'Linden bast': *lênn/iik/pi*. Being compounded from *lênni-*, denoting 'real, original', and *wiik/pi*, 'building material', it indirectly shows that the Delaware did not consider any other 'bast' for the building of their dwellings so long as 'Linden bast', *lênn/iik/pi*, the '*real* building material', was available. In fact, Heckewelder (1888), page 401, in discussing the various household uses of Linden bast in the Delaware community, writes that "a house thus built [that is, with its roof and sides made of Linden bast] is called *lennikgawon*, 'original house or hut'." This term, more explicitly written, **lenn/iik/kâwan*, is a compound from *lênni-*, 'real, original'; *wiik-*, 'structure'; and **woakâwan*, 'a shelter'; with the composite meaning of 'shelter constructed of real building material'. By the way, the Unami term, *wiik/woâm*, 'a house, hut', is contracted from an older form, **wiik/woakâw/an*, specifically denoting 'a *built* shelter', in contrast to 'a *natural* shelter', such as a cave. The latter meaning is fully expressed by **woakâw/an* alone, which is the *generic* term for 'shelter', compounded from *woakâwi*, 'around', and noun suffix, *-an*, with the composite meaning of 'something all around'.

One may be expected to ask: What building material *did* the Delawares use when Linden bast, *lênn/iik/pi*, the *real* thing, was not available? This question, too, can be answered with the aid of semantic analysis. As a Delaware name for 'Elm Tree' (*Ulmus americana* L.) Zeisberger's *Dictionary* lists *âchk/iik/pi*. This term neither describes, nor carries any connotation of, an Elm or

any other tree. In fact, if it were not for its English equivalent listed in the *Dictionary*, one could not possibly tell, from the semantic analysis of the Delaware term, that it functioned as a tree name. The first of its components, *achki-*, a stem with about the same meaning as Eng. 'mock' in, let us say, 'mock turtle soup', indicates that it is not the 'real' thing but rather a 'substitute'. The remainder again is *wiik/pi* 'building material (tree bast)'; thus giving *áchk/iik/pi* the composite meaning of 'substitute material (bast) for building'. This clearly implies that, lacking 'Linden bast', the bast of the American Elm served as a 'substitute' in the erecting of the *wiik/woâm*, 'the man-made shelter (house, hut)'.

As the Delaware generic term for 'tree bark', the *Dictionary* lists Unami *anéchw* (or *anéchkw*), which corresponds to a more explicit Munsee form, **wonáchkw/ew*, denoting 'it is on top'. There is also listed Unami *anechw'/náal/t/ai*, with the definition 'bark canoe'. Since the first component, *anéchw*, signifies *no specific* bark, the compound likewise indicates that it is the *generic* term for 'bark canoe'. Its other components are: *naal-*, a stem denoting 'to fetch'; euphonic *-t-*; and noun suffix, *-ai*; adding up to a composite meaning of 'tree-bark thing to fetch with'.

Next, the question may arise: What trees furnished the bark for the making of canoes? The answer is: Any tree whose bark, or bast, was also used in the erecting of bark huts and houses, such as the Linden and the American Elm. The Paper Birch (*Betula papyrifera* Marsh.) likewise served both these purposes, although farther to the north and northeast than the Tuscarawas Mission area of eastern Ohio. This use of it becomes evident from its Unami name, *wíhin/achk*, or *wín/achk*, both variants being listed in the *Dictionary*. More explicitly written, **wiik/h'/nachkw*, it appears to be compounded from *wiik/heen*, 'to build',and **wonáchkw*, 'tree bark (generic)'; composite meaning: 'tree bark to build with'. Hence, the bark of the Paper Birch, wherever geographically accessible, can safely be claimed as a Delaware building material for both huts and canoes.

There is one more tree whose bark is sure to have been used in the making of canoes, but probably *not* in the building of huts or houses. This is evident from the fact that, in the *Dictionary*, the same term, *wísachk/aak*, in *one* place is listed as the name of the 'Black Oak' (*Quercus velutina* Lam.), and in another as 'bark canoe'. Basically, it doubtless is the name of the tree, for it is a compound of *wísachk/an*, 'something bitter (of taste) ', and *-aak*, a noun affix denoting 'tree (in compounds only) '. The composite meaning is 'bitter tree'. evidently from the bitter taste of its acorns, which nevertheless served as food, after having been processed by boiling. Zeisberger's definition, 'bark canoe', indicates that, besides providing nourishment, the 'Black Oak' was stripped of its bark for the making of canoes; and that the name of the tree was simply applied to the canoe made of this bark.

In view of all these Delaware names of trees which beyond a doubt furnished bark for canoes, it is quite a surprise to find in the *Dictionary* a name for the Tulip Tree, or Yellow Poplar (*Liriodendron tulipifera* L.), which is *amochool/hee*, evidently a shortened form for a more complete **amochool/hée/miinshi*, which, as its analysis will presently show, makes better sense. The term is a compound of *amóchool*, the generic term for 'canoe', with *-heen*, denoting 'to make (in compounds only)' and *-miinshi*, 'tree (in compounds) '. The composite meaning plainly is 'canoe-making tree'. Since there is, however, no reference to, nor any connotation of, 'tree bark (generic)' or 'tree bark (bast)', the canoe made of this tree apparently was *not* a *bark* canoe but rather a 'dugout', that is, a canoe made by hollowing out a tree trunk with fire to a certain depth, and then scraping out the charred wood matter. This technique, which requires no metal tools, has been definitley established for the North American Indians on the aboriginal culture level, and, for the Eastern Forest Indians in particular, in regions where large trees were available, *cf.*, Wissler (1938), page 38; Zeisberger (1910) page 23.

When Daniel G. Brinton, after 1850, had the word material for his *Lenape-*

English Dictionary, of 1888, revised by the Rev. Albert S. Anthony, by birth a Lenape, the latter took exception at some of Brinton's definitions, adding in each case his correction in parentheses. He disagreed, for example, with Brinton's English equivalent, 'poplar', for *amocholhe*, which, in this spelling, had been taken over from Zeisberger's *Dictionary*. Anthony declared *amocholhe*, 'the canoe-building tree', to be "the buttonwood or sycamore", *Platanus occidentalis* L.; *cf.*, Brinton (1888), page 20. Far from being an error on either side, this discrepancy is easily explained. What happened is this: While the Delaware in Zeisberger's Tuscarawas Mission area used the Yellow Poplar, or Tulip Tree, as their 'canoe-making tree', the Sycamore was used for the same purpose by the Mission Indians in southern Ontario, Canada, among whom the Rev. Anthony, at that time, worked as a missioner of the Anglican Church. The Christian Indians in this region, which is well within the range of the Tulip Tree, were in the main Iroquois from New York State and apparently had been accustomed to hollow out their dugouts from Sycamore trunks, continuing to do so in southern Ontario. There, the Munsee converts of the Delaware nation, Rev. Anthony's particular charges, had acquired the use of the Sycamore as their 'canoe-building tree'.

Nothing could better exemplify the following principle: *The Indian name for any tree or plant* (or animal, for that matter) *was never restricted to one particular species but was freely transferred to any other which, under changed conditions, had to serve in the place of that originally used for a given purpose.* Wyman and Harris (1951), page 13, record an analogous observation in their ethnobotanical studies among the Kayenta Navaho.

Although there exists in North America only one indigenous species of Beech, *Fagus grandifolia* Ehrh., Zeisberger's *Dictionary* lists two kinds, which he defines as 'the White Beech', *tanikánimiinshi*, and 'the Red Beech', *sháwemiinshi*. The erroneous notion that 'White Beech' and 'Red Beech' were two separate species rose from the fact that rapid growth, in the Beech, results in much sap wood, which is white; while slow growth results in much heartwood, which is reddish. The Delaware term for the rapidly grown 'White Beech', *tanikáni/miinshi*, apparently is an Unami contraction from a more explicit older form, **tankhakaná/hee/miinshi*, compounded with *tankhakaná heen*, 'to make baskets', and *-miinshi*, 'tree'; composite meaning: 'basket-making tree'. In connection with another tree, Anthony, in Brinton (1888), page 104, remarks that "baskets were made from this, the strips (splints) being obtained by pounding" the wood. This statement about the Delaware's technique in obtaining splint material for baskets, "by pounding" the wood of certain trees, leads to a few essential inferences. In the first place, it helps to explain the otherwise inexplicable Delaware name for 'Red Beech', *sháwe/miinshi*, a compound of *sháwewi*, 'weak', and *-miinshi*, 'tree', meaning 'the weak tree.' As any wood-working artisan will assure us, the slow-grown, reddish heartwood of the Beech is anything but 'weak'. It *is* weak, however, from the standpoint of the basketmaker, because it is hard-fibered and likely to splinter when pounded, but will not make pliable splints as does the rapidly grown *white* beech wood. It is most likely, therefore, that *sháwe miinshi*, 'the weak tree', was a term coined by the Delaware *women*, for they were the basketmakers and, as such, the only ones who could tell from experience that the *reddish* beech wood was *weak*. It can further be inferred that this term belongs to an ancient cultural stratum because, on the later cultural level of wood-working, done by the men, and effectively done only with the metal tools adopted from the whites, these men would never have named this tree 'the weak tree'.

As the makers of splint baskets, those Delaware women practiced an ancient and wide-spread skill. Wissler (1938), page 52, writes, as follows: "Down the Mississippi and south from the Great Lakes, across the Antilles and on into the manioc or Amazon area of South America, basketry has one common characteristic

in that it is made of flat or splint-like materials. . . . North of the Ohio River and in New England where suitable cane was not to be had, we find wood splints in use. They are made from the easily separated annual layers of certain trees. It seems a reasonable assumption that a historical connection exists between those two forms [cane and splint basketry], and since basketry of cane is very widely distributed and materials more readily prepared, we may suspect this to be the parent form."

Another source of basket splints was a tree of the Ash family, whose "easily separated annual layers" were prepared for the purpose "by pounding". Under the definition of 'black ash', Zeisberger's *Dictionary* lists *pachkám/aak*. It doubtless is the Black Ash, also called Hoop Ash, *Fraxinus nigra* Marsh. The Delaware name, *pachkám/aak* is contracted from **pachkánd/'ammen*, 'to beat, pound, maul', affixed with *-aak*, 'tree (in compounds)'; composite meaning: 'the pounding-tree'.

Zeisberger lists 'a Maple Tree' with the Delaware name of *shiichikimiinshi;* according to Anthony, in Brinton (1888), page 128, it is 'the Soft Maple'; either *Acer saccharinum* L., the Silver Maple, or *Acer rubrum* L., the Red Maple; *cf.*, Trees (1949), page 776. Zeisberger's *shiich/hiki/miinshi* (accent uncertain), evidently is a variant (probably Unami) pronunciation of a more revealing **tchiich/hiki miinshi*. Its first component clearly is *tchiich/híkan*, which is listed in the *Dictionary* under two separate headings: 'broom', and 'comb'; the second component is *-miinshi*, 'tree'. Accordingly, the composite meaning is either, 'the broom tree', or, 'the comb tree'. It is not likely that, on the aboriginal culture level, with metal tools not yet in use, wooden combs were made by the Delaware. Hence, the meaning, 'broom tree', is to be given preference. Yet it is not impossible that a stiff hand broom, in between a brush and a comb, was made of 'Soft Maple' twigs for the grooming of human hair, thus rendering the meaning, 'comb tree', likewise acceptable.

The significance of *tchiich-* evidently is 'clean, neat'. In both form and meaning, it appears to be related, if not identical, with *kchiich-*, likewise meaning 'clean'. Added to it is *-híkan*, 'device, tool, to do it with (in compounds only)'. In its last analysis, **tchiich/-hiki/miinshi* means 'device-to-slick-up-with tree'. In this connection it may be noted that the current American slang term, 'a doóhickey' (Webster's New Internat. Dict., 1952), may be a forgotten gift of the Delaware, originally meaning the same as the Delaware term, *-híkan*. This is all the more plausible since, from the very beginning of their contacts with the whites, the Delaware had formed a great many terms for tools, mainly for acquired ones, on this old affix, *-híkan*, as Zeisberger's *Dictionary* amply proves.

Like the Hoop Ash and the Soft Maple a member of the plant association of the river bottoms, 'The Yellow Tree' is listed in the *Dictionary* with two Delaware names: *wisá/miinshi*, and *wisáw/eek*. The former combines *wisáw/ew*, ' (it is) yellow', with *-miinshi*, 'tree'; while the latter combines *wisáw/ew* with *-eek*, a suffix denoting 'that which is'. The one means 'yellow tree'; and the other, 'that which is yellow'. It was obviously named for the yellow dye extracted from it. Its description by Zeisberger (1910), page 52, "The wood is soft and yellowish. The leaves are smooth and somewhat oblong oval," leaves no doubt about its being the Yellow Buckthorn, or Indian Cherry, *Rhamnus caroliniana* Walt. Hough (1907), page 349, states that its "berries, varying from scarlet to black according to degree of ripeness, are . . . sweet and edible," and that "they are ripening in early autumn." They must have possessed a singular attractiveness for the raccoons, for Zeisberger lists still another Delaware name for this tree: *espan/i/miinshi*, with the definitions, 'yellow Wood, or Raccoon Tree'; from *éspan*, 'raccoon'; *-i-* (*-wi-*), copula; and *-miinshi*, 'tree'. Since, according to Zeisberger (1910), page 61, the Indians relished the flesh of the Raccoon as much as they did bear meat, and used its pelt in trading, they also knew, as this latter

tree name clearly indicates, that the best place to hunt it were the Buckthorn trees and bushes, when in early fall the berries were black and sweet.

In the Tuscarawas bottoms, near the Moravian Mission stations of Schönbrunn and Gnadenhütten, there also grew a tree which the *Dictionary* lists as *machtchitkpiak*, with the definition, 'papa', or pappa', as it reads in the Moravian spelling. What is meant is the Papaw Tree, *Asimina triloba* (L.) Dunal. When written, more intelligibly, **machk/tch'/itkpi/-aak*, the following composition presents itself: *máchkew*, ' (it is) red', *tchíttani*, 'strong', *wiík/pi*, 'tree bast', and *-aak*, affix denoting 'tree'; composite meaning: 'tree with red, strong bast'. Hough (1907), page 217, states that "the fibrous inner bark was formerly used for making cord for fish nets." Even Indians living today use this exceedingly strong fiber for various purposes.

The Delaware terms so far discussed were names of trees or tree products which functioned in the Lenni Lenape's aboriginal technology. In analyzing the names of trees which by the English colonists and the German Moravians had been named for the edible wild fruit they bear, this writer has found that frequently the corresponding Delaware terms stress entirely different uses of such trees, with or without an indication that also their fruit was eaten.

A good example for such an indicator of multiple use is the Delaware name, *neesk/achkw/itm/miinshi*, listed in the *Dictionary* with Zeisberger's definition, 'Wild Cherry Tree'. It doubtless is the Wild Black Cherry, *Prunus serotina* Ehrh., which is native to the river bottom of the Tuscarawas valley. The Delaware term is compounded from **neéskew*, ' (it is) filthy';**wonáchkw*, 'tree bark (generic) '; *-iim*, an affix denoting 'fruit', in compounds; and *-miinshi*, 'tree'. Hence, the composite meaning is 'filthy bark-and-fruit tree'. Brinton (1888), in listing a later name, *múi'miinshi*, for 'Wild Cherry Tree', is even more outspoken about the nature of the filth, *mûi-* denoting 'dung'. To appreciate either Delaware name for this tree, one must have watched the birds, mainly American Robins and Cedar Waxwings (the latter also known as Cherry Birds), gorging themselves with black wild cherries, the dark purplish matter running out nearly as fast as it is taken in. It may be noted that the meaning of the aboriginal name, 'filthy bark-and-fruit tree', indicates that both the bark and the fruits were used; the bark, for medicinal purposes, the cherries as food, but also as a dye-stuff.

Another such multiple-use indicator is the Delaware name listed in the *Dictionary* as *woakhattiminshi*, with the definition, 'The Mulberry Tree', which is, of course, the Red Mulberry, *Morus ruba* L., the only native species of the genus. This term, **woak/hatt/itm/miinshi*, is compounded from *woak-*, 'round (curved), bent' (as in *woak/tchínni*, 'to bend') *-hatton*, 'to place, or fix, something'; *-iim*, affix denoting 'fruit'; and *-miinshi*, 'tree'. The composite meaning is: 'fruit-bearing tree used for placing something in curved shape'; specifically, tree-branches, to serve as the framework for bark huts; originally, of the type illustrated in Hodges (1907), I, 518 (bottom of page).

The same connotation is present in the *Dictionary's* term for Dogwood, that is, mainly the Flowering Dogwood, *Cornus florida* L.; it is **hatt/'áwan/o/miinshi'*, compounded from *hatton*, 'to place, or fix, something'; **woakáwan*, 'shelter, hut'; *(-o-* (*-w'-*), copula; and *-miinshi*, 'tree'; composite meaning: 'tree used in placing a hut'. This indicates that the Dogwood served, as did the Red Mulberry, to make of its bent branches the frame of the hut, to which the 'bast' was fastened.

Again with the definition, 'Dogwood', the *Dictionary* lists another term: *moon/hak/an/i/miinshi*. Its composition is clear: *moon/hák/een*, 'to dig the ground' (from *moon-*, stem denoting 'to dig'; *háki*, 'ground'; and *-een*, verb suffix indicating 'action'); *-an*, noun suffix, 'thing', making *moon/hák'an* mean 'a thing to dig the ground with', that is, 'a digging-stick'. Affixed with *-i-* (*-wi-*), copula; and *-miinshi*, 'tree', the composite meaning of the entire term is 'digging-

stick tree'. It implies that the Delaware preferred the Dogwood for the making of digging-sticks, which were an indispensable implement in the planting of Indian corn on the aboriginal level of agriculture, as brought out by Wissler (1938), page 21.

This is another typical case where Anthony, in Brinton (1888), page 86, finds Zeisberger in "error" for his identifying *moon/hak/an/i/miinshi* with 'Dogwood', and declares that the correct definition is "the black haw bush or tree" (*Viburnum prunifolium* L.). Here again, as previously exemplified in these pages (above, page 383), there is no "error" involved, but, under changed conditions, another plant species than that originally used, was applied to a given purpose.

Rather than continue with the analyses of some more of the many tree names at his disposal, this writer wishes to conclude this selection of typical cases by the discussion of two terms which are equally significant technologically and linguistically. Both of them have to do with the patching of damaged bark canoes and huts.

According to a remark in Zeisberger's *Dictionary*, such repair work was done with "the bast (of) the White Elm (which) the Indians use like Hemp and oakum to stop leaks." The tree here mentioned most likely is the American Elm, *Ulmus americana* L. The patching substance referred to is evidently identical with another substance described by Zeisberger (1910), page 23, as "a kind of elm-wood bast which they crush or pound fine and which is of a sticky consistency, serving them in place of tar, to keep their canoes water-tight so that they do not leak." In the *Dictionary*, a Delaware term *améechkwan*, is listed, with the definitions, 'glue', German '*Kleister, Leim*', which seems to denote this very canoe-patching paste. The term, *am/éech/kwan*, more intelligibly written, **am/-'iích/kwoan*, appears to be one of those shortened Unami forms which are contracted almost beyond recognition. Its first syllable, *am-*, suggests *amóchool*, 'a canoe (generic) ', while the remainder, *-'iích/kwoan*, points to **takw/iích/kwoan*, it is joined together'; making a composite meaning of 'the canoe, it is joined together', that is, 'it has been made tight'. 'To patch' is **takw/iich/kwámmen*, while **takw/iich/kwoákan* means 'a patch'.

Another, equally revealing, term for 'glue (patching paste) ' is listed in the *Dictionary* as **m'sukkw/oákan*. It is compounded with **m'súkkw/i* (for **m'súkkw/pi*, really: 'chew matter'), meaning 'spittle'; and *-oakan*, an affix denoting 'substance'; composite meaning: 'substance made with spittle'. This suggests that it was produced by chewing the 'bast' of the Slippery Elm, *Ulmus fulva* Michx., since that bast, when mixed with saliva (*n'sukkw/ándama*, 'I chew'), is known to produce a mucilaginous wad, which, as indicated by the *Dictionary's* definition, 'glue', for **m'sukkw/oákan*, was utilized by the Delaware for repair work by means of glued-on patches.

There is a slight possibility, though, that this chewed-bark patching matter came from a tree, listed in the *Dictionary* as *tó/pi*, with the English definition, 'Alder Tree'. This Unami form, *tó/pi*, could be identified as a contraction of a more explicit, **tákw/pi*, compounded with *takw-*, a stem with the connotation of 'joining (things) together' (*cf.* above); and the affix, *-pi*, denoting 'substance, material to do it with'. This interpretation of *tó/pi* was suggested by an observation of John Josselyn (1672), an early traveler in the American Colonies, telling of an Indian who healed his bruised and cut knee with a compress of chewed Alder bark. This evidently is what the Delaware meant by **tákw/pi* (*tó/pi*), 'join-together substance'. Secondarily, the term also functioned as the name of the tree which furnished the bark: the Speckled Alder, *Alnus rugosa* (DuRoi) Spreng. Although not impossible, yet it is highly doubtful whether this ancient remedy against cuts and bruises was also used for the patching of bark canoes and huts.

SUMMARY

What has been presented in these pages is only a small selection from a comprehensive study along the same lines. When completed, it is hoped that it may furnish some deeper insight into both the culture and the acculturation of the Delaware, if not even, to some extent, of the Eastern Forest Indians in general, in Colonial times.

At any rate, this writer hopes to have presented sufficient proof that his method of semantic analysis as here followed provides the key to the solution of the one or other problem such as arises in the culture study of ethnic groups.

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Biology. *Paul B. Weisz.* McGraw-Hill Book Company, Inc., New York. 1954. xviii+679 pp. $6.50.

This book, intended as a general biology text, is very well done. Its superb organization makes it evident that a great deal of thought went into its preparation. The biologies of plants and of animals, and their inter-relations, are handled in such a way that they form a narrative of remarkably fluid continuity.

Professor Weisz, of Brown University, has chosen to ignore the traditional presentation of countless isolated facts, and writes in terms of general principles of biology.

The book contains many drawings, photographs, and figures, all of which are lucid, and which contribute much to the utility of the book.

The writing of Professor Weisz is notably free from teleological implications, although a few were noted. However, in the long run, the book is remarkable for their scarcity.

The author often resorts to the use of analogies and succeeds in choosing good ones. His treatment of subjects in various "levels" in regard to their complexity is novel and quite effective.

The printer's work should not be overlooked, either. Fairly large type on a good grade of paper makes for easy reading, an the binding is quite simple but very attractive.

The author and the printer have combined their talents in producing a very readable and entirely worth-while work.

ROBERT A. CHAMPLAIN

A PRELIMINARY STUDY OF THE PLANKTON OF THE CLEVELAND HARBOR AREA, OHIO. III. THE ZOOPLANKTON, AND GENERAL ECOLOGICAL CONSIDERATIONS OF PHYTOPLANKTON AND ZOOPLANKTON PRODUCTION[1]

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During the year September, 1950 through September, 1951, a study was made of the Cleveland Harbor area in connection with a survey of pollution conditions in Lake Erie. The chemical and physical results of this study were previously reported by Davis (1953) and Davis and Roney (1953). The results of the phytoplankton analyses were reported by Davis (1954). It is the purpose of the following paper to describe the results of the analysis of the zooplankton obtained in the plankton samples, and in addition to discuss the dynamic interrelations of the plankton and the environment. The relationship of the plankton to pollution is being discussed elsewhere.

Collections and procedures

Twenty-three trips were undertaken between September 15, 1950 and September 30, 1951. Weather conditions permitting, nine stations were occupied as follows (fig. 1):

Station 1. Under the railroad bridge near the mouth of the Cuyahoga River.
Station 2. Between W Pierhead Light and E Pierhead Light at the mouth of the jetties.
Station 3. Halfway between the jetties and Cleveland Division of Water and Heat Intake Crib No. 3.
Station 4. At Intake Crib No. 3.
Station 5. Near red bouy No. 2, off the foot of E 17th St., inside the breakwater.
Station 6. Off the foot of E 40th St., inside the breakwater.
Station 7. Off E Entrance Light, inside the breakwater.
Station 8. Outside the breakwater, opposite station 6.
Station 9. Outside the breakwater, opposite station 5.

At each station, both at the surface and at a depth of 6.5 m. (which was about one meter above the bottom at all stations except the deeper stations 3 and 4), two plankton samples were obtained. At each level one of these samples consisted of approximately 250 ml. of unfiltered water, preserved with 15 ml. of 40 percent formaldehyde, subsequently centrifuged. The second sample was obtained by the use of a Juday plankton trap of 10 liter capacity. This also was preserved with formalin. In addition to the quantitative samples, two qualitative samples were obtained in the cleanest water visited on each trip (usually in the vicinity of stations 4 or 7) by the use of small cone nets made of No. 20 and No. 12 mesh silk bolting cloth. Chemical and physical observations also were made at each station, as described by Davis and Roney (1953) and Davis (1953).

[1]This project was supported by funds allocated by the State of Ohio, administered through the Franz Theodore Stone Institute of Hydrobiology of The Ohio State University, as well as by the loan of essential equipment directly from the F. T. Stone Institute storerooms.

Experience showed that the samples obtained by the use of the Juday plankton trap were more satisfactory, especially for the analysis of the zooplankton. Therefore, except where mechanical failure of the trap, or other misfortune prevented the collection of satisfactory trap samples, the centrifuged samples were not analysed. The report below, except where indicated, is based upon the analysis of the trap samples only.

Trap samples were analysed, in most cases, as follows: the preserved sample was adjusted to a convenient known volume, and a 1 ml. aliquot was placed in a Sedgwick-Rafter plankton counting cell. Common organisms encountered in a given number of the fields delimited by a Whipple ocular micrometer were counted, using the low power (100 X) of a compound microscope. The number of counted fields varied with the abundance of the organisms, and ranged from an occasional

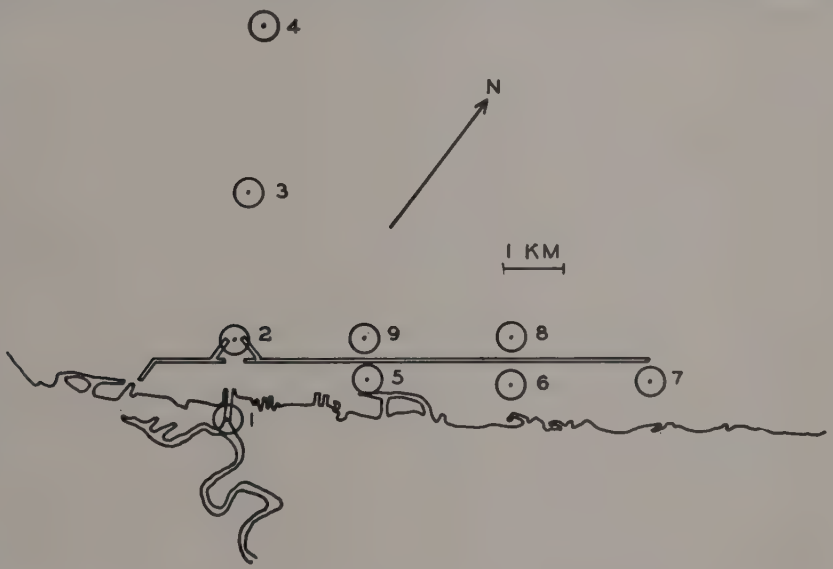


FIGURE 1. Map of the Cleveland Harbor area, showing the location of stations 1–9.

low of 5 to 100 or more. After this preliminary count of the more common plankters, the entire 1 ml. aliquot was examined at the same magnification, and the less abundant forms were enumerated. Where they were sufficiently abundant, the more common larger animal species were counted in a 10 ml. aliquot by the use of a dissecting microscope. Finally, the entire sample was scanned by use of a dissecting microscope and all of the less common larger animal forms were counted.

In those cases where centrifuged samples were used the procedure was similar: a 1 ml. aliquot was analysed carefully by use of the low power of a compound microscope fitted with a Whipple ocular micrometer and the remaining 9 ml. were scanned for larger animals by the use of the dissecting microscope.

Appropriate calculations were then made to estimate the number of phytoplankton cells per liter, and the volumes per liter of the more abundant phytoplankters. Numbers of the zooplankters were estimated per liter or per m^3.

Seasonal distribution of the zooplankton

1. *Total zooplankton.* It was not deemed feasible in this study to determine the volumes of the various zooplankters for two reasons: irregularity of shape

of many of the species (especially Cladocera and Copepoda), and great variability of size among the individuals of many of the species. Lacking determinations of actual volumes, it was advisable to divide the zooplankters into two broad categories, namely those of smaller size (holozoic Protozoa, Rotifera and copepod nauplii), and those of larger size (adult and juvenile Cladocera and Copepoda). Figure 2 shows the seasonal distribution of these two categories of zooplankters, compared with the phytoplankters. Values for larger zooplankters are expressed in numbers per $m.^3$, those for smaller zooplankters are expressed in numbers per liter, and those for phytoplankters are expressed in $\mu^3 \times 10^{-6}$ per liter. All values are averages of all the stations except station 1, which lay in the mouth of the Cuyahoga River, and gave results that were very different from those obtained at the other stations. Consideration of the horizontal distribution of plankters lies beyond the bounds of the present paper, and will be discussed elsewhere.

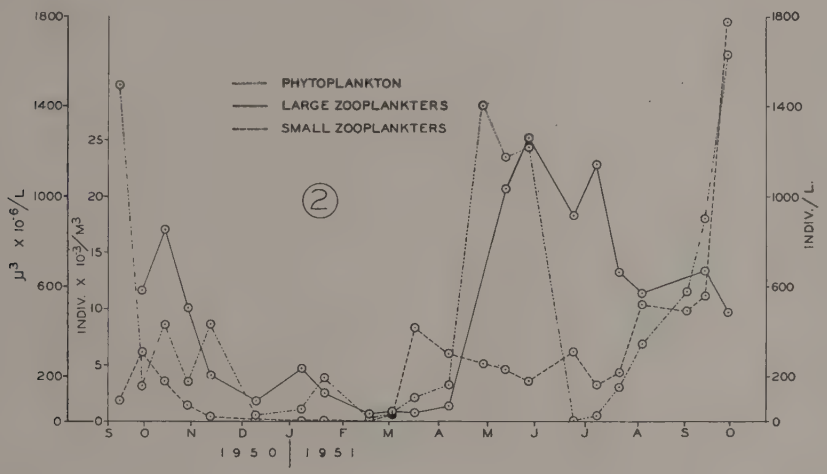
Unlike the phytoplankton, which with some exceptions exhibited a relatively uniform distribution from the surface to the bottom, the zooplankters (especially the Crustacea, but also to a lesser extent the rotifers) were regularly encountered in larger numbers in the deeper samples than in the shallower ones. All samples were taken in the daytime, and as is well known, many species of planktonic Copepoda, Cladocera and Rotifera migrate deeper into the water during periods of relatively intense light. In the discussion below the use of averages tends to even out the inequalities.

As shown in fig. 2, both the larger zooplankters and the smaller forms remained in relatively large numbers during the decline of the autumnal phytoplankton pulse in 1950. During the winter phytoplankton minimum the numbers of both zooplankton categories decreased almost to the disappearing point. The water was most barren of both categories of zooplankters in mid-February and in early March. The spring maximum of the smaller forms occurred in mid-March before the occurrence of the vernal phytoplankton pulse, whereas the spring maximum of the larger forms lagged somewhat behind the peak of the phytoplankton crop. Both groups of zooplankters were very abundant during the summer phytoplankton minimum, but both of them declined in numbers during the continuation of the period of impoverishment. The larger forms continued their gradual decline during the period of the autumnal phytoplankton maximum, while the smaller forms increased enormously in numbers, parallel to the increase of the volume of the phytoplankton. The numbers of smaller forms in September, 1951 were almost three times as great as those at the same date in the previous year, and they were more than twice as great as those obtained during the vernal maximum of 1951.

Elsewhere in Lake Erie, Chandler (1940) is the only author to report the seasonal distribution of total zooplankters. In western Lake Erie in 1938–1939 he found a maximum of about 105 zooplankters per liter in September of 1939, while the vernal maximum in 1939 (at the end of May) was about 130 per liter, and the fall maximum in 1939 was about 1,100 per liter (in September). He encountered a winter minimum (January, 1939) of 3 per liter, and a summer minimum of about 33 per liter. As in the Cleveland Harbor area, the vernal zooplankton maximum lagged behind the vernal phytoplankton pulse. On the other hand, the autumnal zooplankton maxima either preceded (1938) or occurred simultaneously with (1939) the autumnal phytoplankton maximum.

Chandler's results appear to indicate a lower zooplankton production in western Lake Erie at the time of his study than is shown for the Cleveland Harbor area in the present study. Translated to his units, the autumnal zooplankton maximum of 1950 for the Cleveland Harbor area amounted to 320 per liter, while that of 1951 was 1,792 per liter. The January minimum was 6 per liter (hence very close to Chandler's results), but the mid-summer minimum amounted to 186 per liter (early July), which is much higher than that found by Chandler.

Previous to the work of Chandler in western Lake Erie, Wright and Tidd (1933) had reported for the same region that the average number of the commonest Cladocera and Copepoda and of the copepod nauplii for the period between late May and early October was 37 per liter. This compares with an overall average of 14 specimens of the same categories per liter in the present study, during the same portion of the year. Thus Wright and Tidd found over 2.5 times as many of certain zooplankters as reported here. This is commensurate with the greater phytoplankton production of western Lake Erie, as discussed in the previous paper (Davis, 1954).



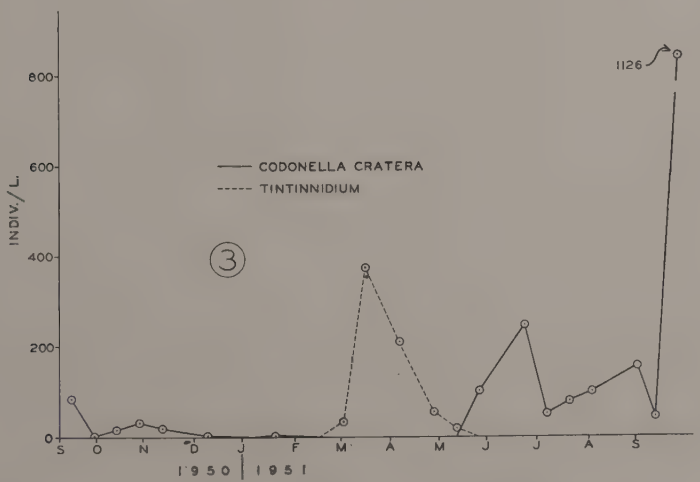


FIGURE 2 Seasonal distribution of smaller zooplankters (holozoic Protozoa, Rotifera and copepod nauplii) in numbers of individuals per liter, and of larger zooplankters (Cladocera and Copepoda) in numbers of individuals x 10^{-3} per $m.^3$, compared with the phytoplankton in μ^3 x 10^{-6} per liter. Values given are averages of all the stations except station 1.

FIGURE 3. Seasonal distribution of *Codonella cratera* and of *Tintinnidium* sp. in number of individuals per liter. Values given are averages of all the stations except station 1.

Elsewhere in Lake Erie, and in the other Great Lakes, quantitative reports on zooplankton populations, or significant portions thereof, have not been presented, or they have been given in a form that is not comparable.

2. *Holozoic Protozoa.* As producers in the ecology of Lake Erie, the holophytic Protozoa were considered in the previous paper (Davis, 1954). Therefore in the present paper only those Protozoa that occupy a position as consumers of particulate organic matter will be considered. This group as a whole exhibited minimal abundance during December, January and February. During this period the average for all stations except station 1 was highest on January 20, but amounted only to 1.5 per liter on that date. Largest quantities were encountered in the spring and in the two autumnal periods, especially the autumn of 1951. The minimum that occurred in the late spring and in the summer was about 75 times as great as the mid-winter minimum.

A number of soft-bodied holozoic Protozoa were observed from time to time. Inasmuch as the preservative had distorted many of them beyond recognition, and none of them occurred in significant quantities at any time, they will not be reported here. *Arcella* and *Difflugia* shells occurred with considerable regularity, especially at station 1 in the River. They were not recorded because these forms are strictly tychopelagic, and furthermore, almost all the shells appeared to be empty shells from deceased organisms.

The tintinnids, *Codonella cratera* and *Tintinnidium* sp. were abundant at times. Their seasonal distribution is shown in fig. 3. The opacity of the tests made it impossible to ascertain in most cases whether the specimens were living or whether empty tests only had been captured. *Codonella cratera* fluctuated greatly from month to month, but only minimal numbers were encountered in December, 1950 and January, 1951, and none at all in February, March, April or the first part of May. In the autumn of 1950 numbers were rather low compared to the quantities estimated for the summer and fall of 1951. *Codonella* exhibited a mid-summer maximum with an average of 248 per liter at the time of the mid-summer phytoplankton minimum. Subsequently the numbers fluctuated, with limited, but not small crops, until on September 30 there was an enormous increase, with an average of 1,126 per liter, and with an absolute maximum of 3,506 per liter at the surface at station 8.

Vorce (1882), under the name *Tintinnus* sp., found this species ". . . during spring, summer and fall, quite abundant at times" in the Cleveland municipal water supply. Elsewhere in Lake Erie, Chandler (1940) reported it from June to September, 1939. The maximum was 66 per liter. It was not mentioned from the eastern basin of Lake Erie by Burkholder (1929a, b). In the other Great Lakes, it was listed as "frequent" in Lake St. Clair by Smith (1894), and the same term was employed by Kofoid (1896) to describe its occurrence in northern Lake Michigan (Traverse Bay area). More recently, Eddy (1927) reported up to 32 specimens per liter from Lake Michigan near Chicago in May, 1927. The same author (Eddy, 1934) said the species was "occasional" in Lake Michigan and in Lake Superior. It can be seen that, of the few quantitative estimates attempted in the Great Lakes, the present one is far greater than any other, especially in the fall of 1951, when the average for all stations except station 1 was about 17 times higher than that reported by Chandler (1940), and about 35 times as great as that reported from Lake Michigan.

Tintinnidium sp. appeared in large numbers only during March, April and the first part of May, 1951 (see fig. 3). The peak was attained in mid-March. An absolute maximum of 1,483 per liter was found at the surface at station 7 on March 17. After May 12 the species was not again encountered in the samples.

Chandler (1940), who is the only author who has carefully studied the year-round distribution of zooplankters in Lake Erie, listed no forms that might correspond with this species. Vorce (1882) encountered and figured a form with

at least a superficial similarity to the present species. He, however, considered it to be a shape variant of "*Tintinnus* sp.", other examples of which were clearly *Codonella cratera.*

Vorticella spp. were regularly encountered in the samples. Typically a benthic genus of Infusoria, some species are epizoic upon planktonic plants, such as *Anabaena.* Because it is not truly a planktonic genus, it was not enumerated in the samples obtained prior to April 6, 1951. Subsequent to that date the genus was counted because of its regular occurrence and relatively large numbers. As would be expected of epizoic forms, the numbers were roughly proportional to the amount of phytoplankton in the water. Largest numbers were found at the peak of the vernal pulse (an average of 134 per liter on April 28), and during the autumnal pulse (averages of 288 per liter on September 3; 229 per liter on September 14; and 152 per liter on September 30). Lowest numbers were found during the summer phytoplankton minimum, with an average of only 5 per liter on June 23.

In western Lake Erie, Chandler (1940) found the genus in most collections, "but not exceeding 15 per liter". In the eastern basin, Burkholder (1929a, b) reported it to be the most abundant protozoan in the plankton, with a maximum of 571 per liter in August, 1928. This maximum is similar to that obtained in the present study (600 per liter on September 3 at the surface at station 6).

3. *Rotifera.* As shown in fig. 4, the rotifers were most abundant in the two fall seasons and in late spring. Their fluctuations in numbers seemed to be more closely correlated with phytoplankton volumes than in the case of other major constituents of the zooplankton. Maximum quantities found during the entire study were on August 4, 1951, when there were 330 per liter, and at the end of September, 1951, when there were 490 per liter.

In the same general area of Lake Erie, Metcalf (1942) estimated the numbers of Rotifera at two stations off Lakewood in June, August and September of 1939. His method of collection precludes an accurate comparison of results. He reported rather large numbers in June, namely from 37 to 1,024 per liter, with the average of three collection dates at two stations being 398 per liter. His results for August and September are shown only graphically, but there was a maximum of about 37 during this period. Elsewhere in Lake Erie, Chandler (1940) found a seasonal distribution of total rotifers similar to that encountered in the present study. There was a maximum of 45 per liter in the autumn of 1938, a maximum of 75 per liter in May, 1939, and a maximum of 250 per liter in late September, 1939. Thus other quantitative estimates from Lake Erie are similar to those obtained in the Cleveland Harbor area in the present study.

Keratella cochlearis was the most common of the rotifers in the present study. Figure 4 shows the seasonal distribution of the species, numbers being averages per liter of all stations except station 1. The seasonal fluctuations of abundance are similar to those for all species of rotifers together. Highest average values were encountered at the end of September in each year. The absolute maximum was 956 per liter at the surface at station 7 on September 29, 1950.

A record was kept of the numbers of individuals bearing eggs, and these numbers are also depicted on fig. 4. At the end of September, 1950 and during October, from 3.4 to 12.1 percent of the individuals carried such eggs. Thereafter until May of the following year practically no reproducing specimens were seen, and the total number of individuals decreased greatly. During May the rate of reproduction increased to 21.2 percent. By the end of June, however, total numbers of this species were very small, and no evidence of reproduction was observed. Towards the end of July the total number of individuals had increased to 9 per liter, and the reproduction rate reached its peak for the year, namely 46 percent. This rapid reproductive rate resulted in a great increase of individuals, so that on the trip of August 4 there was an average of 247 individuals per liter. The reproductive rate and the total numbers then remained high in September.

Chandler (1940) found *K. cochlearis* to be among the most abundant of the rotifers of western Lake Erie, exhibiting a pulse in the fall of 1938 and another in the fall of 1939. There was a maximum of 150 per liter in September, 1939. Vorce (1881) said it was "common" in the Cleveland water supply. It was one of the two most abundant rotifers in Terwilliger's Pond (Ahlstrom, 1934), with important vernal and autumnal pulses. Ahlstrom estimated a maximum of 1,750 per liter in October. According to Kellicott (1896), it was "extremely abundant" in the water supply of Sandusky. In the eastern basin of Lake Erie, Burkholder (1929a, b) found the species to be "rather frequent" in July, but it was missing in September. He gave a maximum of 81 per liter in mid-August.

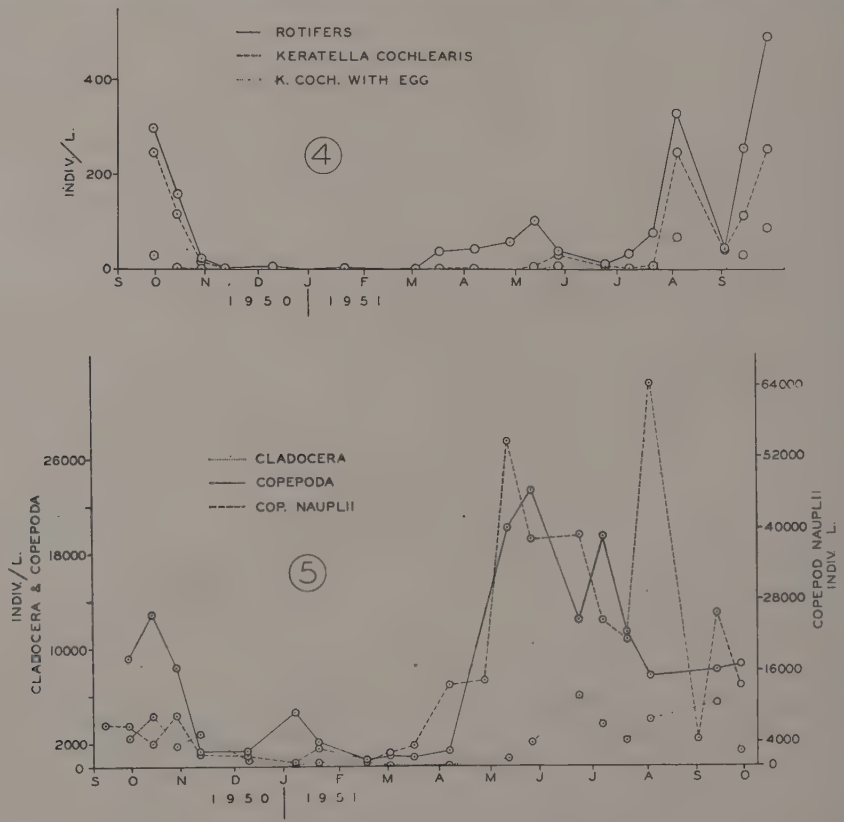


FIGURE 4. Distribution of total rotifers, of *Keratella cochlearis*, and of *K. cochlearis* with eggs in number of individuals per liter. Values given are averages of all the stations except station 1.

FIGURE 5. Distribution of Cladocera, of Copepoda, and of copepod nauplii in number of individuals per m.^{3}. Values given are averages of all stations except station 1.

In the other Great Lakes, Jennings (1894) noted that it was "one of the most abundant" planktonic rotifers in Lake St. Clair. The same author (Jennings, 1896) found it more frequently than any other planktonic rotifer in northern Lake Michigan. Similarly, Ahlstrom (1936) recorded it to be "the most important species of rotifer numerically" in Lake Michigan. Previously Eddy (1927) had reported a maximum of 17 per liter of this species in Lake Michigan waters in the vicinity of Dunes Park. The species was listed by Eddy (1934) as "occasional" in Lake Michigan and "common" in Lake Superior.

In addition to *Keratella cochlearis*, the following rotifers were observed more or less commonly: *Asplanchna* sp., *Conochilus unicornis*, *Filinia longiseta*, *Keratella quadrata*, *Notholca longispina*, *N. striata*, *Polyarthra* spp., and *Synchaeta* spp. Table 1 sketches their seasonal distribution and gives a brief comparison with other records in the Great Lakes.

TABLE 1

Occurrence of Rotifera, other than Keratella cochlearis

Species	Period of occurrence (months)	Maximum abundance (numbers per liter in parentheses)	Other records, Great Lakes (numbers per liter in parentheses)
Asplanchna sp.	1950: S., D. 1951: S.	1950: S. 29.	Erie: Kellicott, '97 (very common) Chandler, '40 (4) St. Clair: Jennings, '94 (very abundant) Michigan: Jennings, '96 (very abundant)
Conochilus unicornis	1951: Jn., Jl.	1951: Jl. 7 (ave. 7; max. 36)	Erie: Burkholder, '29 (very common) Ahlstrom, '34 (45) Chandler, '40 (32) St. Clair: Jennings, '94 (very common) Michigan: Ahlstrom, '36 (very common)
Filinia longiseta	1951: My.	1951: My. 12.	Erie: Kellicott, '96 (not uncommon) Ahlstrom, '34 (900) Chandler, '40 (10) Michigan: Eddy, '27 (8)
Keratella quadrata	1951: Ap., My.	1951: My.	Erie: Chandler, '40 (6) Michigan: Eddy, '27 (8.5)
Notholca longispina	1950: N. 1951: Ma., My., Jn., Jl., S.	1951: My. 26 (ave. 5.5; max. 18)	Erie: Vorce, '81 (common) Kellicott, '97 (common) Chandler, '40 (18) St. Clair: Jennings, '94 (very abundant) Michigan: Jennings, '96 (regularly) Eddy, '34 (occasional) Ahlstrom, '36 (never commonly) Superior: Eddy, '34 (common)
N. striata	1951: My.	1951: My. 12 (ave. 7.5; max. 30)	Erie: Ahlstrom, '34 (55) Chandler ,'40 (6) Michigan: Ahlstrom, '36 (sparingly)
Polyarthra spp.	1950: S., O. 1951: My., Jn., Jl., Au., S.	1950: O. 13 (ave. 31) 1951: My. 12 (ave. 9), S. 14 (ave. 87; max. 275), S. 30 (ave. 123)	Erie: Vorce, '82 (common) Kellicott, '96 (common) Burkholder, '29 (408) Ahlstrom, '34 (2,218) Chandler, '40 (50) St. Clair: Jennings, '94 (commonest) Michigan: Jennings, '96 (frequent) Eddy, '27 (16) Eddy, '34 (occasional) Superior: Eddy, '34 (occasional)
Synchaeta spp.	1951: Ma., Jl., Au., S.	1951: Jl. 21 (ave. 43; max. 84). S. 30 (ave. 9)	Erie: Kellicott, '97 (plentiful) Burkholder, '29 (small numbers) Ahlstrom, '34 (2,420) Chandler, '40 (70) St. Clair: Jennings, '94 (very abundant) Michigan: Ahlstrom, '36 (very common)

4. *Cladocera.* The seasonal distribution of the total Cladocera, including both juveniles and adults, is shown in figure 5. Few specimens were present in winter and in spring. During May the numbers increased, and on June 23 the maximum for the entire year was observed, amounting to an average of 5,870 per m.^{3} This maximum occurred at the time of the lowest point of the mid-summer phytoplankton minimum. The cladoceran population decreased, but not excessively, during the remainder of the summer. It increased again in August and September, but at the end of September, 1951 the population had decreased to a level somewhat below that observed at the same time in the previous year. During October and November (1950) the population fluctuated, but decreased steadily towards the winter low.

The production of Cladocera in the Cleveland Harbor area during the year September, 1950 through September, 1951, was apparently comparatively low. In the region of Greater Cleveland, in the summer of 1939, Metcalf (1942) estimated an average of 82,314 per m.^{3} at two stations on three dates in the latter half of June (max. 219,600 per m.^{3}). During August and September he found a maximum of about 45,000 per m.^{3} As mentioned above, Metcalf's methods were only semiquantitative. In the western basin, Wright and Tidd (1933) calculated an average of 5,000 per m.^{3} for the entire period from late May to early October in 1929 and 1930. Chandler (1940) reported an average of 4,400 per m.^{3} for the period from September to mid-December, 1938, and an average of 5,000 per m.^{3} during the period from May 23 to September 25, 1939. In the eastern basin Wilson (1929a, b) showed the presence of large numbers of Cladocera, but his samples were not obtained quantitatively.

The distribution of the several species of Cladocera is shown in Table 2, along with a summary of the observations of other authors in the Great Lakes. The taxonomy of the genus *Daphnia* remains in an unsatisfactory state, as attested by various authorities, such as Wesenberg-Lund (1926), Brooks (1946) and Pennak (1953). No clarification can be brought to these matters here, and for the present purposes it is thought sufficient, following the example set by Chandler (1940), to distinguish three clearly defined forms, listed here as *Daphnia longispina, D. pulex* and *D. retrocurva*. Kiser (1950) would place the second and third forms as variants of a single species, and there is considerable indecision in the literature (Wesenberg-Lund, 1926; Berg. 1931, etc.), as to the propriety of separating *D. longispina* from *D. pulex*. The distribution of these three species of *Daphnia* in the Great Lakes is peculiar. *D. pulex* appears to be considerably less important in western Lake Erie than it is in the central and eastern basins. In Lake Ontario it has been listed as common, but the species has never been reported from any of the upper Great Lakes. Its abundance in Lake Winnipeg (Bajkov, 1930) indicates that its absence from the upper Great Lakes is not associated with latitudinal or geographic differences. The environmental factors preventing its occurrence need careful examination. The other two species occur more widely. An investigation of their quantitative distribution among the several Great Lakes would be of greatest interest.

5. *Copepoda.* The seasonal distribution of adult and juvenile copepodid stages of the Copepoda is shown on figure 5. The distribution of copepod nauplii is shown separately on the same figure. Largest numbers of the copepods occurred in the spring, lagging somewhat behind the development of the vernal phytoplankton pulse. The peak occurred on May 26, when the average was 23,240 per m^3. Relatively large numbers were also encountered during the period of the summer phytoplankton minimum, and during the fall months, and there was a small pulse during January.

Nauplii had a somewhat similar distribution, with, however, the greatest numbers in early August, 1951 (an average of 64,300 per m.^{3}). During the vernal maximum the copepod nauplii began to increase greatly in numbers before the

TABLE 2

Occurrence of Cladocera

Species	Period when most common (months)	Maximum abundance (numbers per m^3 in parentheses)	Other Great Lakes records (max. number per m^3 in parentheses)
Bosmina longirostris	1950: S., O., N., D. 1951: My., Jl., Au., S.	1950: S. 29 (ave. 100), O. 27 (ave. 200), N. 11 (max. 1,500). 1951: My. 12 (ave. 260), My. 26 (ave. 400; max. 1,600), Au. 4 (ave. 350; max. 1,200), S. 14 (ave. 600; max. 1,900).	Erie: Vorce, '81 (common) Wilson, '29 (common) Chandler, '40 (10,000) St. Clair: Birge, '94 (constant) Georgian Bay: Sars, '15 (not infrequent) Michigan: Eddy, '27 (most abundant)
Ceriodaphnia reticulata	1951: My.	1951: My. 26.	Erie: Chandler, '40 (small numbers)
Chydorus sphaericus	1951: My., Jl., Au., S.	1951: Au 4.	Erie: Vorce, '82 (common) St. Clair: Birge, '94 (always present) Georgian Bay: Bigelow, '22 Michigan: Eddy, '34 (occasional) Superior: Forbes, '91 (frequent) Eddy, '34 (rare)
Daphnia longispina	1950: S., O. 1951: S.	1950: S. 29 (ave. 1,400; max. 13,600), O. 13 (ave. 2,500; max. 5,300). 1951: S. 14 (ave. 1,500; max. 7,200).	Erie: Bigelow, '22 (very abundant) Wilson, '29 (important) Chandler, '40 (most abundant—9,000) Ontario: Bigelow, '22 (very abundant) Georgian Bay: Bigelow, '22 (most abundant) Superior: Eddy, '34 (common)
D. pulex	1950: S., O. 1951: My., Jn., Jl., Au., S.	1950: O. 13 (ave. 900) 1951: Jn. 23 (ave. 2,200; max. 12,300), Jl. 7 (ave. 2,400; max. 5,700), Au. 4 (ave. 980), S. 14 (ave. 1,660; max. 5,300).	Erie: Wilson, '29 (most abundant) Chandler, '40 (3,000) Ontario: Bigelow, '22 (common)
D. retrocurva	1950: O. 1951: My., Jn., Jl., Au., S.	1951: Jn. 23 (ave. 3,600; max. 10,700), Jl. 21 (ave. 1,140; max. 5,500), Au. 4 (ave. 1,700; max. 4,300), S. 14 (ave. 850).	Erie: Bigelow, '22 (very abundant) Wilson, '29 (common) Chandler, '40 (4,000) Ontario: Bigelow, '22 St. Clair: Birge, '94 (frequent) Georgian Bay: Sars, '15 (rather common) Bigelow, '22 (abundant) Michigan: Eddy, '27 (300) Superior: Forbes, '91 (large numbers) Eddy, '34 (occasional)
Diaphanosoma leuchtenbergianum	1950: O. 1951: Jl., Au., S.	1950: O. 13 (ave. 310). 1951: Au. 4 (ave. 600), S. 14 (ave. 650; max. 2,400), S. 30 (ave. 300).	Erie: Chandler, '40 (3,000) Georgian Bay: Bigelow, '22 Michigan: Eddy, '27 (common)
Leptodora kindtii	1950: S., O. 1951: Jl., S.	1950: O. 27 (max. 400)	Erie: Bigelow, '22 (important) Chandler, '40 (1,000) Andrews, '48 St. Clair: Birge, '94 Georgian Bay: Sars, '15 (rather common Bigelow, '22 Michigan: Forbes, '82 Eddy, '27, '34 Superior: Forbes, '91

increase of the adults and copepodids, even preceding slightly the inception of the vernal phytoplankton pulse. The vernal peak of nauplii occurred in mid-May, with an average of 54,600 per m.^{3}

Metcalf (1942) studied the occurrence of copepods in the region of Greater Cleveland in 1939. His methods were only semi-quantitative, and were not fully comparable to the methods used in the present study. In 6 samples obtained at two stations in the latter half of June he estimated an average of 202,500 per m.^{3} (max. 951,500 per m.^{3}). During August and September he showed a maximum of about 60,000 per m.^{3} In the western basin of Lake Erie, Wright and Tidd (1933) calculated an average for the entire period from late May to early October (1929 and 1930) of 16,000 copepods and 16,000 nauplii per m.^{3} In the present study the averages for the same portion of the year are 12,490 copepods and 22,600 nauplii per m^3. In the western basin Chandler (1940) found copepod pulses in autumn and spring in 1938 and 1939. In September, 1938 he reported a maximum of 40,000 per m.^{3} The spring pulse of 1939 extended from early April to mid-July, with a maximum of 70,000 per m.^{3} in late June. The summer minimum (in July) amounted to 20,000 per m.^{3}, in contrast to the winter minimum of only 2,000 per m.^{3} The fall maximum of 1939 amounted to 40,000 per m.^{3} He described a similar seasonal distribution for copepod nauplii, with a maximum in late June of 40,000 per m.^{3} The results obtained by Wright and Tidd compare rather closely with the Cleveland Harbor area results, but Chandler found a larger quantity of copepods.

In the eastern basin of Lake Erie, Wilson (1929a, b) studied only non-quantitative samples. He found that copepods were less important in bulk than the Cladocera.

The seasonal distribution of the several species of copepods is shown in table 3, where previous records from the Great Lakes are also listed. No attempt was made to identify juvenile copepodid stages of the Cyclopoida, nor of *Diaptomus*. Attempts to separate the species of female Diaptomus in the counts were considered unreliable, and therefore only males are reported quantitatively as separate species.

TABLE 3

Occurrence of Copepoda

Species	Period when most common (months)	Maximum abundance (numbers per m^3 in parentheses)	Other Great Lakes records (max. number per m^3 in parentheses)
Canthocamptus staphylinoides	1951: My., S.	1951: My. 26 (max. 200)	Erie: Chandler, '40 (1,000) Michigan: Eddy, '27 (4,225) Superior: Forbes, '91
juvenile Cyclopoida	1950: S., O., D. 1951: My., Jn., Jl., Au., S.	1950: S. 29 (ave. 5,900; max. 20,400), O. 13 (Ave. 4,600), O. 27 (ave. 4,000). 1951: My. 12 (ave. 4,700), My. 26 (ave. 12,100; max. 23,600), Jl. 21 (ave. 7,000), S. 14 (ave. 4,000).	
Cyclops americanus	1951: Jl., S.	1951: S. 30.	Erie: Chandler, '40 (3,000) Andrews, '53 (17, 760)
C. biscuspidatus	1951: Ja., Mar., Ap., My., Jn.	1951: Ap. 6 (ave. 330), My. 12 (ave. 500; max. 1,800), My. 26 (ave. 500; max. 1,000).	Erie: Wilson, '29 (common) Chandler, '40 (7,000) Andrews, '53 (11,000) Great Lakes: Marsh, '95 (the common species) Georgian Bay: Sars, '15 (not infrequent) Michigan: Forbes, '82 (excessively abundant) Eddy, '27 (4,225) Superior: Forbes, '91 (the commonest) Eddy, '34 (common)

TABLE 3—(Continued)

Species	Period when most common (months)	Maximum abundance (numbers per m^3 in parentheses)	Other Great Lakes records (max. number per m^3 in parentheses)
Mesocyclops leuckarti	1950: S., O. 1951: My., Jn., Jl., Au., S.	1950: O. 13 (ave. 1,000; max. 1,900) 1951: Jl. 21 (ave. 520; max. 3,200), S. 30 (ave. 620; max. 2,700).	Erie: Chandler, '40 (6,000) Andrews, '53 (2,540) St. Clair: Marsh, '95 Georgian Bay: Sars, '15 (common) Michigan: Marsh, '95 Superior: Forbes, '91 (moderate numbers)
juvenile *Diaptomus*	1950: S., O. 1951: My. Jn., Jl., Au., S.	1950: O. 13 (ave. 6,000). 1951: My. 12 (ave. 12,300; max. 19,200), My. 26 (ave. 4,200), Jn. 23 (ave. 5,600), Jl. 7 (ave. 10,400; max. 19,600); S. 30 (ave. 3;900).	
Diaptomus spp. ♀	1950: S., O., D. 1951: Ja., Mar., Ap., My., Jn., Jl., Au.	1950: O. 27 (ave. 800). 1951: Ja. 5 (ave. 1,700), Jn. 23 (ave. 2,220; max. 4,200), Jl. 7 (ave.3,300; max. 9,300).	
D. ashlandi ♂	1950: O. 1951: Ja., Mar., Ap., My., Jn., Jl., Au.	1951: Ja. 5 (ave. 900), Ja. 20 (ave. 700), Jn. 23 (ave. 1,000; max. 2,700), Jl. 7 (ave. 1,700; max. 10,000)	Erie: Wilson, '29 (numerous) Chandler, '40 St. Clair: Marsh, '95 (not abundant) Michigan: Marsh, '95 (common) Eddy, '27 (2,000) Superior: Marsh, '93 Eddy, '34
D. minutus ♂	1951: Mar., Ap., My., Jl.	1951: Ap. 6 (max. 700), My. 12 (ave. 150), Jl. 7 (ave. 120).	Erie: Chandler, '40 St. Clair: Marsh, '95 (most common) Georgian Bay: Sars, '15 Michigan: Eddy, '27 (1,600) Superior: Eddy, '34 (common)
D. oregonensis ♂	1950: S., O. 1951: Jl., Au.	1950: O. 27 (ave. 1,000; max. 2,800). 1951: Jl. 7 (ave. 150), Au. 4 (ave. 100).	Erie: Chandler, '40 Great Lakes: Marsh, '95 (not abundant) Georgian Bay: Sars, '15 (abundant)
D. sicilis ♂	(throughout the year)	1951: Ja. 5 (ave. 950; max. 1,700), Ap. 6 (ave. 200), Ap. 12 (ave. 300), Jl. 7 (ave.300).	Erie: Wilson, '29 (abundant) Chandler, '40 Michigan: Forbes, '82 (immense numbers) Superior: Forbes, '91 (most abundant)
D. siciloides ♂	1951: Jl., Au., S.	1951: Jl. 7 (ave. 100; max. 800)	Erie: Chandler, '40
Epischura lacustris	1950: S., O. 1951: My., Jn., Jl., Au., S.	1951: My. 26 (ave. 600♂, 400♀ 4,200 juv.; max. 3,000♂ 1,900♀, 12,900 juv.).	Erie: Wilson, '29 (never very abundant) Chandler, '40 (8,000) St. Clair: Marsh, '95 (common) Michigan: Forbes, '82 (considerable numbers) Marsh, '95 (common) Superior: Forbes, '91 (common)
Limnocalanus macrurus	1951: Ja., Mar., My., S.	1951: Ja. 20 (max. 300), My. 12 (max. 700).	Erie: Chandler, '40 (1,000) Detroit River: Marsh, '95 Michigan: Forbes, '82 (abundant) Superior: Forbes, '91

DISCUSSION

In the previous paper (Davis, 1954), the sparsity of quantitative phytoplankton data for the Great Lakes was noted. The poverty of quantitative information on the zooplankton is even more striking. Only Chandler (1940) has seriously attempted to make a year-round quantitative study of all the zooplankters. Andrews (1953) made a careful study, but of three species only. Metcalf (1942) attempted a semi-quantitative study during a brief portion of the year in the Greater Cleveland area of Lake Erie. He contented himself with only three categories of zooplankters: Rotifera, Cladocera and Copepoda. Furthermore, his collections were made with an open net. Ahlstrom (1934) made a careful quantitative study of rotifers in Terwilliger's Pond, but not in Lake Erie proper. Elsewhere in the Great Lakes, only Eddy (1927)[2] has attempted a quantitative investigation. Eddy confined himself to a few quantitative collections at several different points in southern Lake Michigan during October, 1926 and May and July, 1927. In all other published studies, where the authors have gone beyond the simple approaches of taxonomy and distribution, only subjective estimations of abundance were made. Our lack of knowledge is the more regrettable, for it is commonly agreed that the North American Great Lakes constitute the largest and economically most important mass of strictly fresh water on the face of the earth.

The present results indicate a somewhat higher overall standing crop of zooplankton in the Cleveland Harbor area of 1950–1951 than that found by Chandler (1940) in the western basin in 1938–1939, but this apparently was the result of a relatively large number of the (volumetrically less important) smaller zooplankters in the present study. In an earlier year, Wright and Tidd (1933) had indicated larger zooplankton crops than comparable figures reported here. Their results were based upon only a limited portion of the zooplankton, namely the larger forms and copepod nauplii. Similar comparisons with other of the Great Lakes cannot be attempted.

In any study such as this it is the standing crop of the plankton that is determined, rather than the rate of plankton production, be it the phytoplankton or the zooplankton. Furthermore, when a series of stations at fixed locations is visited periodically, different water masses are being sampled on each visit. At times in the present study, totally different water masses were sampled at the outside stations, as compared with those closer inshore. For example, on January 20, 1951, at station 4, the volume of the total phytoplankton was between 6 and 7 times as great as that encountered at the other stations that were visited (Davis, 1954). On this date at the same station the average volume of *Melosira* sp. alone was 633×10^6 μ^3 per liter, while the average of all the other stations together was 57.6×10^6 μ^3 per liter. Thus at station 4 there was 11 times as much *Melosira* as the average at all the other stations. It is clear that at least two separate water masses were being sampled on that day. The nature of the investigation made it impossible to ascertain either the extent of such water masses or their movement and fate between collecting trips. More will be said below on this matter in connection with an attempt to interpret the sequence of plankton production.

An adequate interpretation of the seasonal changes of the plankton content of any body of water depends upon viewing the standing crop as the result of a dynamic series of events. The existing quantities (and the proportional quantities) of the plankton are the present status of its continuing development out of the standing crop of the past and into the standing crop of the future. Many

[2]Quantitative plankton analyses were reported by Tressler et al. (1953) for Irondequoit Bay, off Lake Ontario. Irondequoit Bay is nearly closed off from Lake Ontario, and there is no free circulation of water between the bay and the lake.

influences come to bear upon plankton production: physical factors such as temperature, density, diffusion currents, horizontal currents, turbulence, amount of solar radiation, turbidity, ice cover, etc.; chemical factors such as pH, quantity of plant nutrients, oxygen content, presence of trace elements, quantity of non-nutrient ions, the ratio of free CO_2: HCO_3^- : $CO_3^=$, etc.; and biological factors such as quantity and nature of available organic food, quantity and nature of enemy organisms, interspecific and intraspecific cooperation and competition, matabolic rate, life span, rate of reproduction, etc. As pointed out by Wautier (1949) in his excellent discussion of these ecological principles:

"Si l'on tente de préciser les raisons de la complexité du milieu physique, on constate qu'elles sont multiples. Chaque facteur n'agit pas isolément, mais en liaison avec les autres. Les actions ne s'ajoutent pas mais se combinent, chaque facteur agissant sur tous les autres et étant, á l'inverse, affecté par chacun d'eux. Les differents facteurs n'interviennent d'ailleurs pas tous de manière forcément simultanée; certains peuvent avoir agi antérieurement a d'autres, favorisant, modifiant ou contrecarrant leurs effets. Il y a plus: l'action de certains facteurs modifie plus ou moins la sensibilité des organismes à d'autres facteurs."

The response of a species to one factor often varies as other factors change. In the previous paper (Davis, 1954), for example, the diatom *Asterionella* sp. was shown to be present in the plankton throughout the year. During most of the time it was subordinate to other diatoms in quantity, but during much of the winter and early spring season it was the dominant phytoplankter. This condition has also been observed in the western basin of Lake Erie (Chandler, 1940, 1942, 1944; Chandler and Weeks, 1945). One might infer from all this that *Asterionella* production was favored by the cold water conditions of winter and early spring. On the other hand, during the period of the spring phytoplankton maximum in the Cleveland Harbor area, when temperatures were rising rapidly, *Asterionella* remained present in approximately the same numbers (with a slight decrease) as before the vernal pulse (see Davis, 1954, fig. 15). It is conceivable that the temperature conditions of late spring were even more favorable for this species than the cold of winter, but that other factors, such as the antagonistic effects of other phytoplankters, or competition for plant nutrients in the period of enormous phytoplankton production, retarded its production.

Asterionella was practically absent during the summer months, but this could not have been the result of the deleterious effects of high water temperatures, as indicated by the fact that with the reduction of the zooplankton at the beginning of August, *Asterionella* produced its biggest standing crop of the year (though it was subordinate to other forms). At the beginning of August the water temperature stood at its seasonal peak. The estival sparsity of *Asterionella* must have been caused by other factors, such as the high grazing rate of the myriads of zooplankters present at that time.

Similarly, the copepod, *Diaptomus ashlandi* occurred in largest quantities in mid-winter and in mid-summer, though it was present at all times of the year. The large number in mid-summer undoubtedly was associated with the great production of phytoplankton during the warm months, but the potential numbers probably were not attained because of stiff competition from other larger zooplankters (especially *Daphnia*). During the winter there was little competition from other zooplankters, and *D. ashlandi* was thus able to take advantage of a relatively small phytoplankton pulse at that time. The lack of a pulse of adult *D. ashlandi* during the periods of the spring and of the fall phytoplankton maxima may have been associated with breeding activities, which were not determined in this study. The spring phytoplankton maximum was preceded by $2\frac{1}{2}$ months of low phytoplankton production, which would be detrimental to the development of nauplii and other juveniles of *D. ashlandi*. Furthermore, active breeding in the near-freezing temperatures of January does not appear probable (few females of *Diaptomus* with egg cases were observed at that time). If the females were

as abundant as the males in mid-summer (this was the case for females of all species of *Diaptomus* together, and *D. ashlandi* males were the most abundant of all species of the genus), and if they bred commensurate with their numbers, then it is possible that their numerous offspring succumbed in large numbers a) to a relative lack of food during late July, and b) to a large increase of planktonic and other predators as a result of the enormously rich food supply of midsummer. The increase of predators is suggested by the fact that the predator *Leptodora kindtii* was most common during September.

Such explanations as those above are necessarily hypothetical in the present state of our knowledge, but the hypotheses can be tested by more adequate field studies, and it is planned to make such studies in the future.

The striking nature of the seasonal fluctuations of the phytoplankton and the zooplankton has led inevitably to a number of attempts to unravel the intricacies of cause and effect that are involved. Some of the early workers (e.g., Apstein, 1896), as well as some more recent, have observed the small quantities of plankton during the cold months of the year, and the large masses of blue-green and green algae often occurring in the warmest months, and have concluded that the controlling factor for phytoplankton production, and hence indirectly for zooplankton production, is the temperature of the water. On the basis of other evidence, however, other early authors concluded that it is not the temperature, but solar radiation that is the controlling factor. This is the stand taken, for example, by Zacharias (1907). Still other authorities have adopted a somewhat more dynamic point of view, namely that the basic causative factor is neither the temperature nor the radiant energy directly, but changes in the plant nutrient content of the water. According to this third conception, the spring and fall overturns refresh the nutrients by a mixture of the nutrient-rich deeper layers of water with the nutrient-poor upper layers, hence allowing the vernal and autumnal phytoplankton pulses to occur. The rapid growth of the phytoplankton depletes the nutrient salts and results in the summer or winter phytoplankton minimum. Different quantities and proportions of the important minerals (nitrates, phosphates, silicates, etc.), favor different groups of phytoplankters (diatoms, greens, blue-greens, etc.). Among the foremost proponents of the plant nutrient hypothesis are Pearsall (1932), and Rodhe (1948).

The voluminous accumulation of data from the study of many sorts of lakes and ponds in many countries has forced most recent authors to abandon the attempt to explain seasonal fluctuations on the basis of any one controlling factor. This data includes, for example, the work of Chandler (1940), who showed that the entire vernal phytoplankton pulse of 1939 in western Lake Erie occurred beneath the ice cover, and hence at winter temperatures. In the present study there was a marked mid-January phytoplankton and zooplankton pulse, when water temperatures were only a fraction of a degree above freezing, and when solar radiation was at a minimum. Many lakes, including western Lake Erie, and at least that portion of the central basin reported here, almost never exhibit temperature stratification, and hence there are no vernal and autumnal overturns. Frequently such lakes have marked vernal and autumnal phytoplankton pulses. Furthermore, many temperate zone lakes do not have regular spring and fall maxima, as shown by Pennak (1946, 1949) in certain Colorado reservoirs.

The "stubborn facts" have forced aurhors in recent years to adopt generalizations that reflect the interaction of more than one factor. Findenegg (1947) and Steleanu (1953) stressed the interaction of both temperature and light. According to Findenegg, the winter plankton population consists of cold-water, weak-light species, the spring population of cold-water, strong-light species, the summer plankton of warm-water, strong-light species, and the fall plankton of warm-water, weak-light species. In the present study, both the vernal and autumnal phytoplankton maxima were dominated by *Melosira* sp. (Davis,

1954), and as mentioned above, *Asterionella* sp. dominated the winter phytoplankton, but there was a much larger biomass of this form at the peak water temperatures in the early fall. According to Findenegg's scheme, *Melosira* must therefore be both a cold-water, strong-light form and a warm-water, weak-light form, and *Asterionella* must be placed in the cold-water, weak-light category, or in the warm-water, strong-light category, depending upon the season.

Innate internal rhythms of reproduction, nutrient supply, and seasonal flooding have been suggested as causative agents by Carpenter (1928), who concluded that some local factors probably always contribute to the complex influences affecting plankton production. Needham and Lloyd (1937) correlated temperature, spring and fall overturns and grazing by zooplankters as influences in seasonal phytoplankton fluctuations The interaction of the rate of multiplication and the rate of depletion was discussed by Ruttner (1952) and Ruttner, Frey and Fry (1953). These authorities suggested that the rate of multiplication is determined largely by the combination of the two factors of Findenegg—solar radiation and temperature—, but they added that plant nutrients are important. The rate of depletion is influenced primarily by sinking and sedimentation, modified by the water inflow and outflow, and through consumption by grazers and predators.

Recently McCombie (1952) has reviewed the literature concerning the influence of physical, chemical and biochemical factors on phytoplankton quantity. Although the body of his paper clearly indicates the complexity of the interactions of the several factors, he follows the tendency towards oversimplification that dominates much biological thought today by concluding: ". . . this cycle is caused chiefly by the seasonal change in water temperature resulting from the change in solar radiation."

After summarizing many of the theories concerning the causes of seasonal fluctuations of the plankton, Welch (1952) drew the only feasible conclusion: that it is probably impossible to use any single factor or influence to explain the periodic maxima and minima, but that the fluctuations are the result of the interplay of influences acting in combination and at different intensities. Such conclusions, however, remain vague generalizations unless the principles are illustrated by concrete applications to actual seasonal cycles. Even Wautier (1949), whose clarity on these matters is unsurpassed, inadvertently discouraged further research into these matters when he figuratively threw up his hands in dismay and stated:

> "Un telle complexité du milieu physique rend tres difficiles, dans l'état actuel de la science, l'analyse rationelle et la compréhension, même partielles, des relations entre le milieu et les organismes."

Certainly our knowledge has advanced to the stage where we may profitably attempt to analyze the interplay of influences determining the seasonal fluctuations of plankton abundance.

In the following such an analysis will be attempted to explain the general progress of events during the year in the Cleveland Harbor area. Each of the hypotheses that is suggested can easily be tested through a planned program of further field observations and laboratory culture experiments. At this time explanations of the fluctuations of abundance of individual species will not be attempted, but only the fluctuations of large groups. Figure 2 of the present paper shows graphically most of the events under consideration. Other figures should also be consulted.

In the fall of 1950 there was a large standing crop of phytoplankton, and of zooplankton as well, though the latter apparently had not at first reached its autumnal maximum. During October and early November the water temperatures fell rapidly (Davis, 1953; Davis and Roney, 1953), and solar radiation

decreased sharply. This inevitably resulted in a reduction of the rate of metabolism and of reproduction among the phytoplankters. At the same time there was a considerable increase of the zooplankton, perhaps because of a reduction of the number of predators. As a result primarily of these three factors, the phytoplankton declined in importance, so that by early December the winter phytoplankton minimum had firmly set in. Quantities of the zooplankton, especially the larger forms, declined more slowly (along with the decrease of their food supply), but by early December these also had declined to their first winter minimum.

During January, both the phytoplankton and the larger zooplankton forms increased to a mid-winter maximum, but peculiarly, the zooplankton maximum preceded the phytoplankton maximum. This may have been caused by the sampling of different water masses in early January as compared to late January—water masses concerning whose history we have no evidence—, or it may indicate that phytoplankton productivity in early January was higher than that indicated by the measurements of the phytoplankton standing crop. In the latter case the zooplankters would keep the phytoplankton crop grazed down, but with the disappearance of the bulk of the zooplankters (through old age, predators, starvation, etc.), the phytoplankton would increase to its mid-winter pulse. More detailed study of mid-winter productivity is needed to clarify this problem.

In March the increase of solar radiation, probably with other factors, appears to have increased the productivity of the phytoplankton considerably. This was indicated, not by any great increase of the standing crop of the phytoplankton, though there was a slight increase. Rather, it was indicated by a considerable increase in the quantity of the smaller zooplankters. This increase preceded by 6 weeks the vernal phytoplankton maximum. On the other hand, because of the slower breeding rate of the larger zooplankters, their vernal maximum lagged behind the vernal phytoplankton maximum by two weeks. It is interesting to note in this connection that copepod nauplii and cladoceran embryos (in their parental brood pouches) increased strikingly in abundance *before* the vernal phytoplankton pulse, but adults of these two groups, and copepodid stages of the Copepoda, did not increase greatly until after. Possibly the slight decline of the smaller zooplankters during the period just before and during the vernal phytoplankton maximum was the result of competition with the growing population of nauplii, and later of older stages of Copepoda and Cladocera.

As described in the previous paper (Davis, 1954) the decline of the vernal phytoplankton maximum was very sudden and precipitous. It would seem improbable that such a sudden and complete change could take place in such a short period in a single water mass. Therefore it is postulated that around the first of June a new water mass, barren of phytoplankters, encroached upon the Cleveland Harbor area from farther west in the lake. Presumably the same general changes would have taken place in the previous water mass, however, given sufficient time.

With the disappearance of the vernal phytoplankton maximum the mid-summer maximum of larger zooplankters appeared, associated with the rich food supply of the previous period. It seems apparent that there was no decrease of phytoplankton productivity, despite the sparsity of the standing crop, contrary to the stated or implied assumptions of most previous authors (e.g., Welch, 1952). It would seem that the large quantity of actively feeding zooplankters kept the standing crop decimated by incessant grazing, and in reality phytoplankton productivity remained as high, or nearly so, as before. The effect of grazing in the development of the mid-summer phytoplankton minimum has been suggested previously by Needham and Lloyd (1937).

During the summer and ensuing fall the numbers of the larger zooplankters steadily decreased, possibly in connection with competition for the existing food,

and with the increase in the number of predators such as *Leptodora kindtii*. Ultimately this decline reached a point where phytoplankton production again exceeded phytoplankton destruction, and the autumnal phytoplankton maximum set in. The increase in available food, and the reduced competition of large zooplankters then allowed the smaller zooplankters, with their short life histories, to increase enormously.

In all the above, an important direct grazing effect of the zooplankters is assumed, following the example of Riley, Stommel and Bumpus (1949). Some recent authors have cast doubt upon such a direct effect of grazing (see Pennak, 1946), but important experimental and observational work, some of it very recent (e.g., Pennington, 1941 and Bainbridge, 1953), supports the contention that the zooplankters graze directly upon both the larger phytoplankters and the nannoplankters, and thus directly affect the size of the standing crop of the phytoplankton. The results of the present study cannot adequately be explained other than on the basis of a direct grazing effect.

The above analysis leaves many questions unanswered, especially questions about the fluctuations of individual species, but also such questions as the great difference between the fall season of 1950 and that of 1951 as regards the production of smaller zooplankters (fig. 2). It also is undoubtedly true that many important influences have been omitted from the discussion. For example, Lefévre, Jakob and Nisbet (1952) have proven the importance of self-produced antibiotics in the growth of plankton algae, as has Rice (1954). Factors such as this may have had an influence in the decline of phytoplankton pulses. Many authors have emphasized the necessity of plant nutrients (see above). It is possible that increased nutrients entering the lake with the spring run-off influenced the development of the vernal phytoplankton maximum, and that decreased nutrients influenced the development of the estival minimum. These matters need to be examined further for clarification. In this connection, Juday *et al.* (1928) have shown in certain Wisconsin lakes that as much phosphorus was present in the summer as during the spring phytoplankton maximum, and that there was no increase of the phosphorus content of the water just preceding the vernal phytoplankton pulse. In the present results, there was a marked mid-winter phytoplankton pulse (Davis, 1954, and fig. 2 above), supporting the contention that low nutrient content was not the primary cause of the winter minimum. A continuing zooplankton maximum during the summer phytoplankton minimum is clear evidence of continuing phytoplankton production, and hence of adequate quantities of plant nutrients. An additional influence—that of turbidity—is sometimes important in limiting plankton production. In the present study, turbidities were measured (Davis, 1953; Davis and Roney, 1953), but there was no apparent correlation with plankton crops.

It is planned to follow up as many of these problems as time permits.

SUMMARY

1. The results of the analysis of quantitative zooplankton samples taken on 23 trips at nine stations in the Cleveland Harbor area of Lake Erie are given. The trips were undertaken in the year September, 1950 through September, 1951. Previously there has been only a single year-round quantitative study of the zooplankton in the Great Lakes. This was the study by Chandler (1940) in the western basin of Lake Erie.

2. The larger zooplankters (Cladocera and Copepoda) occurred in largest numbers during the summer period, when the phytoplankton was at its summer minimum. There were, however, large numbers also in both autumn seasons, and there was a small pulse (mostly Copepoda) in mid-winter. The quantity of these larger zooplankters appears to be smaller than that reported from the western basin.

3. The maximum of larger zooplankters in the fall of 1950 and that setting in during the late spring of 1951 lagged behind the occurrence of the phytoplankton maxima.

4. The smaller zooplankters (holozoic Protozoa, Rotifera, and copepod nauplii) were most abundant in the spring of 1951, and in both fall seasons. The spring maximum was larger than the maximum of September, 1950, but the fall maximum in 1951 (late September) was many times greater than either of the other two. The quantity of the smaller zooplankters in the Cleveland Harbor area considerably exceeded the quantities reported from the western basin.

5. The maxima of the smaller zooplankters tended to accompany the occurrence of the maxima of phytoplankton, or they even preceded the diatom maxima. Thus, the vernal maximum of 1951 occurred in late March, 6 weeks before the vernal phytoplankton maximum.

6. The seasonal distribution of the various species of holozoic Protozoa, Rotifera, Cladocera and Copepoda are tabulated, and compared with the results of other observers elsewhere in the Great Lakes. In general, the larger species occurred in smaller quantities than in the western basin of Lake Erie, while some of the smaller species occurred in larger quantities.

7. The effects of the diurnal vertical migration of the planktonic Crustacea was evident in the unequal distribution of these forms between the surface samples and the samples collected at 6.5 m. All samples were collected in the daytime, and the deeper samples averaged much larger numbers of these forms.

8. The necessity of distinguishing standing crops of plankton from plankton productivity is emphasized. Also, in such studies as the present one, it is pointed out that different water masses are sampled on every collected trip, and sometimes even on one collecting trip at different stations. Examples are given from the results.

9. An attempt is made to analyze the course of events in plankton production during the year. The complexity and interplay of the influences is stressed. The seasonal history of the diatom genus *Asterionella* and of the copepod *Diaptomus ashlandi* are used as examples of the manner in which the influence of one environmental factor varies as other environmental factors are altered. The decline of the autumnal phytoplankton maximum is thought to be the result of lower reproductive rates and a great amount of grazing by zooplankters. A great increase of phytoplankton production was indicated in March by a considerable increase in smaller zooplankters, 6 weeks before the onset of the vernal phytoplankton pulse. The decline of the vernal phytoplankton maximum is thought to have been caused primarily by the heavy grazing activity of the numerous zooplankters during the summer months. The onset of the autumnal phytoplankton maximum is thought to have been caused by a reduction of the larger zooplankters, which in turn was caused by a combination of a reduction of the food supply and an increase in the numbers of predators.

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ERRATA

Due to an omission in article by Josef N. Knull in the Ohio Journal of Science, 54: 1954, the following paragraph should be inserted after line 17 on page 296.

Holotype male, allotype and paratypes collected by D. J. and J. N. Knull at Jacumba, San Diego Co., Calif., July 6 and one paratype, July 9, all 1952.

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